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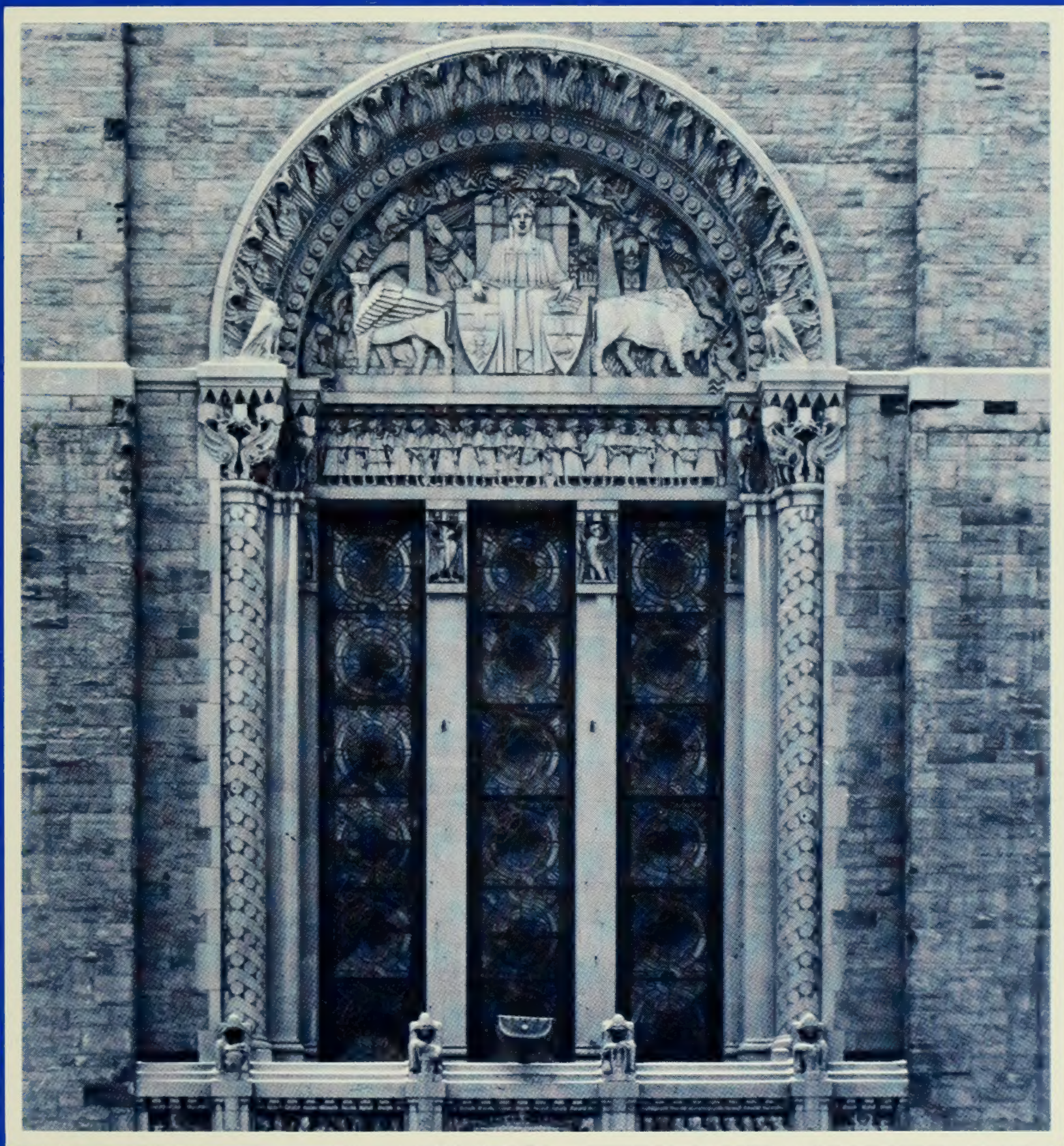

The Status of *Smilodontopsis* (Brown, 1908) and *Ischyrosmilus* (Merriam, 1918)

A Taxonomic Review of Two Genera of Sabretooth Cats (Felidae, Machairodontinae)

C. S. Churcher

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Contents

The Status of *Smilodontopsis* (Brown, 1908) and *Ischyrosmilus* (Merriam, 1918)

Abstract

The sabretooth genus *Smilodontopsis* Brown, 1908 is a junior synonym of *Smilodon* Lund, 1842. Distinctive fossils from Port Kennedy Caverns, Pennsylvania, described as *Machaerodus (Smilodon) gracilis* and *M. (S.) mercerii* by Cope (1880, 1899) are referred to *Ischyrosmilus* Merriam, 1918. *Ischyrosmilus gracilis* (including *I. mercerii*) is distinct from *Smilodon* and *Homotherium* Fabrini, 1890 (including *Dinobastis* Cope, 1893) and includes specimens from Florida, Texas, Nebraska, Idaho, and California. *Ischyrosmilus* is intermediate structurally between *Megantereon* Croizet and Jobert, 1828 and *Smilodon*. *Ischyrosmilus johnstoni* Mawby, 1965 includes materials from *Homotherium crenatidens* Fabrini, 1890.

Newly recovered materials from Bass Point Waterway I and El Jobean Pit, Florida, the type specimen of *Machaerodus (Smilodon) gracilis* from Port Kennedy Caverns, Pennsylvania; and reassessments of described specimens assigned to *Smilodon gracilis* or to species of *Ischyrosmilus* provide bases for the taxonomic revision.

Key words—sabretooth cats, taxonomy, Quaternary, North America, Felidae, Machairodontinae, Smilodontini, Homotheriini, *Machaerodus, Smilodon, Megantereon, Smilodontopsis, Ischyrosmilus, Homotherium, Dinobastis, I. gracilis, H. serum*.

Introduction

This taxonomic review is concerned with three problems: (1) the status of the generic name *Smilodontopsis* Brown, 1908; (2) the identities of specimens usually referred to as *Smilodontopsis gracilis* or *Smilodon gracilis*; (3) the relationships of *S. gracilis* with the North American genus *Ischyrosmilus* Merriam, 1918, the New World genus *Smilodon* Lund, 1842, and the Holarctic genera *Machairodus* Kaup, 1833, *Megantereon* Croizet and Jobert, 1828, and *Homotherium* Fabrini, 1890.

The genus *Smilodontopsis* dates from Brown's original description of specimens from the Conard Fissure, Arkansas, in 1908. His two species *Smilodontopsis troglodytes* and *S. conardi* were characterized by the possession of an entepicondylar foramen on the humerus, in which they were to differ from the South American genus *Smilodon* Lund, 1842, probably on the uncited authority of Gervais (1878) and Cope (1899). *S. troglodytes* was distinguished from *Felis (Trucifelis) fatalis* Leidy, 1868 (= *Smilodon fatalis*) by its relatively larger and well-developed metacone on the upper carnassial. Brown (1908:189) noted that the upper carnassial lacks a protocone, the parastyle is large and high, and the prostyle or "preanterior cone is a well-developed tubercle, but not as large as in *Trucifelis fatalis*, although the tooth is much longer" mesiodistally.

Brown (1908) distinguished between *S. troglodytes* and *S. conardi* on two features: a shallower median depression on the buccal face of the metacone and a better-developed paracone on the upper carnassial. Merriam and Stock's (1932) study of a large series of teeth of *Smilodon californicus* Bovard, 1907 from Rancho La Brea, California, demonstrated that these two features are highly variable. Consequently they concluded that Brown's recognition of two sabretooth species from the Conard Fissure was unfounded and recognized only *S. troglodytes*.

Cope described *Machaerodus (Smilodon) gracilis* and *M. (S.) mercerii* in 1899 from Port Kennedy Caverns, Pennsylvania, as lightly built cats within the general North American lineage of Pleistocene sabretooths. Merriam and Stock (1932) suggested that these species might be more closely related to *Smilodontopsis* than to *Smilodon* and included them within the former genus as a subgenus of *Smilodon*. They also recognized only one species, *S. gracilis*, from the Port Kennedy Caverns. In their (1932) classification of the North American Pleistocene sabretooths, Merriam and Stock placed all species within the genus *Smilodon* but assigned the subgenus *Trucifelis* to include *S. fatalis* Leidy, 1868, *S. floridanus* Leidy, 1889, *S. californicus* Bovard, 1907, and *S. nebrascensis*

Matthew, 1918. *Smilodontopsis* was also reduced to subgeneric rank to include *S. troglodytes* Brown, 1908 (including *S. conardi* Brown, 1908), *S. gracilis* (Cope, 1880), and *S. mercerii* (Cope, 1899), both of which had been originally described as *Machaerodus (Smilodon) gracilis* and *M. (S.) mercerii* and whose specific distinction they questioned. They also included *Dinobastis* as a third subgenus of *Smilodon* to bring *Dinobastis serus* Cope, 1893 within the genus. Simpson (1945) followed Merriam and Stock's (1932) scheme without change, placing the three subgenera within *Smilodon* Lund, 1842.

Slaughter (1963:80) reviewed the known species of *Smilodon* and concluded that *Dinobastis* constituted a genus separate from *Smilodon:* "There appears to be but three well defined species of *Smilodon* in North America, *S. gracilis, S. floridanus,* and *S. fatalis.*" He also synonymized *S. californicus* with *S. floridanus*. Churcher (1966) defined the generic distinctness of *Dinobastis* from *Smilodon* and concluded that *Dinobastis* is a junior synonym of *Homotherium* Fabrini, 1890.

Kurtén (1965) accepted Slaughter's taxonomy in general and considered *S. gracilis* to be a smaller Yarmouthian sabretooth from which evolved the subsequent Illinoian, Sangamon, and early Wisconsin *S. fatalis* (including *S. trinitiensis* Slaughter, 1960). He considered *S. floridanus* to be a synonym of *S. fatalis,* and *S. californicus* the most progressive form, even when compared with Floridan specimens of the same age, and thus apparently a valid species.

Webb (1974) accepted Slaughter's taxonomy but differed from Kurtén in considering *S. californicus* to be a synonym of *S. floridanus*. Subsequent workers (e.g., Robertson, 1976) generally followed similar taxonomic schemes and referred to the smaller sabretooth as *Smilodon gracilis* and to the larger as *S. fatalis* or *S. floridanus*.

Kurtén and Anderson (1980) recognized *Smilodon gracilis* as taxonomically intermediate between *Megantereon hesperus* and *Smilodon fatalis* and included all other smilodont sabretooths within *S. fatalis,* with at best, subspecific status. They separated *Ischyrosmilus* as an incompletely known genus with an unknown number of species and stated (1980:188–189) that the known specimens "may represent a single lineage of a sexually dimorphic form with a tendency to size increase and gradual reduction of anterior premolars. . ." and that it may derive from *Machairodus* and also be related to *Homotherium*. They accepted *Homotherium serum* as distinct from the smilodonts and possibly derived from the Old World *H. latidens* or North American *H. crenatidens* and also possibly distantly descended from *Machairodus*.

Martin (1980) placed "*M. gracilus*" (*sic*) with *Megantereon* rather than *Smilodon* on the presence of a functional P_3 in the former genus. He also considered *Ischyrosmilus* to be a synonym of *Homotherium,* and *Homotherium* to be distinct from *Dinobastis*.

This paper attempts to demonstrate that the holotype of *Machaerodus gracilis* and other specimens assigned to *Smilodon gracilis* represent members of the tribe Smilodontini and that *M. gracilis* is congeneric and probably conspecific with the described species of *Ischyrosmilus*. Its status is considered intermediate between ancestral *Megantereon hesperus* and descendant *Smilodon fatalis* on temporal and evolutionary criteria.

Methods

TOOTH NOMENCLATURE

Individual teeth are identified by a nomenclatural and positional shorthand that gives the type of tooth, its position in the sequence, and whether upper or lower and milk or permanent. Each full notation consists of four elements:

1. l or r indicate left or right sides of the arcades.
2. i, c, p or I, C, P, and M indicate whether incisors, canines, premolars, or molars, with lower case letters indicating milk teeth, and upper case permanent teeth.
3. 1, 2, 3, or 4 indicate whether first, second, third, or fourth members of a morphological group within incisors, canines, premolars, and molars.
4. Superscript or subscript positions of the indices 1–4 indicate position in upper or lower jaws respectively.

Thus "lp^3" indicates the left milk upper third premolar and "rM_1" the right lower first permanent molar. The term "milk molar" is not used since such teeth are molarized milk premolars and referred to as p3 or p4, when either upper or lower and left or right quadrants are equally probable.

Within the text other nomenclatural systems are cited, and these are variants of the one used here. Milk teeth may be indicated by "d" placed before an upper case I, C, or P, as in "dC^1" for the milk upper canine or sabre, and permanent teeth by the absence of the "d". Brown (1908:191) used "p_4" and "m_1" to indicate permanent lower teeth, whereas I use "P_4" and "M_1". Merriam (1918:524) used "$P_{\bar{3}}$" and "$P_{\bar{4}}$" with the bar reinforcing the lower jaw position of these premolars.

DENTAL TERMINOLOGY

All teeth have four orientations of the crown's sides: lingual or internally towards the tongue, buccal or labial or

externally towards the cheek or lips, mesial or along the dental arcade towards the midline (equivalent to anteriorly on some cheek teeth), and distal or along the dental arcade towards the condyle (equivalent to posteriorly on some cheek teeth). On first or central incisors, mesial is the same as medial and distal as lateral, but on first molars, lingual is the same as medial and buccal as lateral.

The standard system of cusp terminology in which terms for the upper teeth end in *-cone, -style, -loph,* etc., and for the lower teeth in *-conid, -conulid, -lophid,* etc., is used throughout.

Upper cheek teeth are assumed to have three basic cusps arranged in a trigon (triangle)—mesiobuccal paracone, distobuccal metacone, and lingual protocone. Subsidiary conules, e.g., paraconule, may also be present. Lower cheek teeth are assumed to have a similar but reversed trigonid (triangle), with buccal protoconid, mesiolingual paraconid, and distolingual metaconid. Distal to the trigonid may occur an accessory expansion of the crown known as the talonid (heel).

The noncarnassialized premolars have three main cusps in line: mesially a paracone (-id), centrally a protocone (-id), and distally a metacone (-id). Additional enamel thickenings mesially or distally are called shelves or cingula. Incisors have a single main cusp, the protocone (-id), with subsidiary small paracone (-id) and metacone (-id) cuspules mesially and distally. Canines have only single cusps, the protocones (-ids).

Ridges running along the thin crests of cusps are referred to as the mesial or distal ridges or crests of the cusp. On upper canines that are expanded to form sabres, the surfaces are referred to as the buccal and lingual faces or surfaces, and the crests as the mesial and distal margins or crests. Cusps in which expansion to form a shearing blade has occurred (carnassialization) are referred to as the protocone blade, paraconid blade, and metaconid blade.

Roots that directly support cusps may be referred to as protoradix, pararadix, etc., for roots directly beneath the protocone (-id) or paracone (-id).

REGISTRATION OF SPECIMENS

Specimens mentioned in this report form parts of the collections of a number of institutions and are identified by catalogue numbers composed of a letter prefix and a numeral. The letter prefix identifies the following institutions:

AMNH	American Museum of Natural History, New York, N.Y.
ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania.
B	Brayfields' Collection, El Jobean, Florida.
FDT	Florida Diving Tours, Ocala, Florida.
LACM	Los Angeles County Museum of Natural History, Los Angeles, California.
ROM	Royal Ontario Museum, Toronto, Ontario.
ROM:B	Royal Ontario Museum (Bass Point Waterway I), Toronto, Ontario.
ROM:P	Royal Ontario Museum, Vertebrate Palaeontology Collection, Toronto, Ontario.
TMM	Texas Memorial Museum, University of Texas, Austin, Texas.
UC	University of California, Department of Geology, Berkeley, California, now catalogued as UCMP (see below).
UCMP	University of California, Museum of Paleontology, Berkeley, California.
UF	University of Florida, Florida State Museum, Gainesville, Florida.
UNSM	University of Nebraska State Museum, Lincoln, Nebraska.
USNM	National Museum of Natural Sciences (United States National Museum), Washington, D.C.
WT	West Texas State College, Panhandle Plains Historical Museum, Canyon, Texas.

All units given are metric unless otherwise specified. Dimensions are given in millimetres (mm) unless otherwise specified.

Materials

This section comprises annotated inventories of the specimens that have been included within *Smilodontopsis, Smilodon gracilis,* and *Ischyrosmilus* and which are considered in the "Discussion".

CONARD FISSURE SPECIMENS

Brown's (1908) description of *Smilodontopsis troglodytes* and of *Smilodontopsis conardi* from the Pleistocene deposits of the Conard Fissure, 15 miles (24 km) south of Harrison, Arkansas, constituted the first use of this genus and descriptions of the species. Brown (1908:188) founded the genus *Smilodontopsis* on the type species *S. troglodytes,* which comprised specimens catalogued as AMNH 11786 and included the "point of an upper canine, an upper sectorial and an upper incisor; three vertebrae, distal end of humerus, distal ends of radius and ulna and olecranon process of ulna, several carpals, tarsals, metacarpals and phalanges", which were described. The second species, *S. conardi,* was founded (Brown, 1908:190) on a "complete carnassial, greater part of crown of the upper canine and lower canine", catalogued as AMNH 11790. Brown referred several bones and teeth,

catalogued as AMNH 11792 and 11785, to the latter species. He described a "p_3, two other separate p_3, a fourth (?lower) premolar, and a lower carnassial m_1" and "several dissociated fragmentary limb bones, carpals, metacarpals and a part of associated pes are referred to (*S. conardi*) although they pertain to *Smilodontopsis troglodytes* equally well". These elements comprise three unciforms, three metacarpals (Mc)—one McII and two McV—phalanges, a partial tibia, calcaneum, astragalus, navicular, ectocuneiform, and four metatarsals. Two partial dentaries are catalogued as AMNH 11785 but are not described, although the teeth are probably described.

Examination of the specimens in the American Museum of Natural History, New York, revealed more specimens than Brown listed and also a different arrangement by species and catalogue numbers. As it is impossible to recognize with confidence the specimens that Brown mentioned, I shall list them as catalogued when examined by me. Inconsistencies occur, e.g., the absence of a lower canine, which may have been misidentified and be represented by an I^2, the absences of P_3, P_4, and M_1, and the partial mandible AMNH 11785, part of which may be present within AMNH 11786.

The materials of *S. troglodytes,* catalogued as AMNH 11786, comprise: right upper permanent first incisor (rI^1); left upper permanent canine or sabre (lC^1); right upper permanent fourth premolar or carnassial (rP^4); fragment of a left dentary with condyle and part of a left dentary with part of the mandibular canal, probably constituting one dentary; three partial lumbar vertebrae, possibly III, IV, and V; distal ends of left ulna, left radius, and left humerus; fragment of ?left navicular; parts of proximal end, shaft, and distal articulation of left metacarpal III; three distal articulations of metapodials, one with some shaft; two unidentifiable proximal ends of metapodials; right astragalus; two digital sesamoids; four entire and two fragmentary proximal phalanges; three entire and three fragmentary middle phalanges; and four damaged ungual phalanges.

The species *S. conardi* was described at the same time and founded on three isolated teeth, catalogued as AMNH 11790: right upper permanent second incisor (rI^2), possibly identified as a lower canine by Brown; crown of left upper permanent canine or sabre (lC^1); and left upper permanent fourth premolar or carnassial (lP^4).

Additional elements are catalogued as AMNH 11782 (and 11785 in Brown, 1908:190), noted as "Postcranial of *S. conardi?*", and comprise: distal ends of right humerus and left ulna; left scapholunar lacking sesamoid process; left and right unciforms; right pisiform; distal end of tibia; right calcaneum; left and right proximal phalanges of digit I.

Associated with these identified and catalogued specimens are two catalogued and six uncatalogued specimens from the same deposit. Some may be listed by Brown within either *S. troglodytes* or *S. conardi* but are identified in the collections only as "*Smilodon*". They comprise: crown of right upper permanent first incisor (rI^1); partial crown of right upper permanent sabre or canine (rC^1); mesial part of right upper permanent fourth premolar or carnassial (rP^4); two single-rooted right permanent third lower premolars (rP_3's); left unciform and scapholunar lacking pisiform facet (AMNH 11787); and proximal articulation of proximal phalanx of digit I.

When these catalogued and uncatalogued specimens are assessed to determine the minimum number of individuals from which the entire Conard Fissure sample of sabretooths could have derived, only two individuals are required. Possibly one has been described as *S. troglodytes* and one as *S. conardi,* although the skeletal elements are probably mixed in all three samples.

Certain characteristics of these two individuals are evident: both P_3's are single-rooted, and the mesial and distal serrations on the margins of the sabres are of the same type and have the same degree of development as seen in sabres of *Smilodon.* The upper carnassial fragment assigned to *S. troglodytes* (rP^4, AMNH 11786) lacks any remnant of a protocone, and the entire tooth assigned to *S. conardi* (lP^4, AMNH 11790) possesses a very small tubercle above the protoradix identical to that present on the partial upper carnassial (rP^4, uncatalogued) tentatively assigned to "*Smilodon*".

The sabretooth materials collected by Brown from the Conard Fissure derive from at least two individuals of a large cat similar to *Smilodon* in all respects. The single-rooted condition of P_3's and the presence of rudimentary protocones on two upper carnassials are both conditions that are not unknown in other isolated specimens of *Smilodon* and occur in some individuals of *S. californicus* (Merriam and Stock, 1932:48–51).

CAVETOWN SPECIMEN

Hay (1920) described the new species *Smilodontopsis mooreheadi* on an isolated right upper carnassial (rP^4, USNM 9212) from Cavetown, Washington County, Maryland. Dimensions of this tooth were given as: mesiodistal length, 26.5; paracone height, 14; metacone height, 9.5; paracone width, 11.5; and metacone width, 8 mm (Hay, 1920:107). This specimen was said to be smaller than the same tooth in *S. conardi* or *Machaerodus gracilis* and was considered to resemble P^4 of *Felis inexpectata.* Simpson (1941) re-examined this specimen and concluded that it originated from a puma, probably *F. inexpectata,* with which I agree.

PORT KENNEDY SPECIMENS

Cope (1880) described *Machaerodus (Smilodon) gracilis* and later (1899) *M. (S.) mercerii* on the remains of gracile

sabretooths recovered from Port Kennedy Caverns, Pennsylvania. These specimens were considered by Merriam and Stock (1932) to constitute their revised subgenus *Smilodontopsis* and to be distinct from the Rancho La Brea *Smilodon californicus,* but they questioned the validity of the second species. The deposit is considered to be late Pliocene or early Pleistocene and represents the early Irvingtonian faunal age (Kurtén and Anderson, 1980). The Port Kennedy specimens are catalogued in the Academy of Natural Sciences of Philadelphia as ANSP 44–51. No types were designated by Cope, although a broken sabre was the specimen on which *M. (S.) gracilis* was first described (Cope, 1880), and isolated cheek teeth rP_4 and lP^3 (ANSP 50) those on which *M. (S.) mercerii* was described (Cope, 1899).

The specimens of *Machaerodus (Smilodon) gracilis* Cope, 1880 (= *Smilodontopsis gracilis* [Cope] of Merriam and Stock, 1932) comprise:

ANSP 44. Crushed and distorted facial region of a skull and mandible, with all four tooth rows but lacking upper molars (M^1's), right lower canine (rC_1) and third premolar (rP_3). Cope (1899, pl. 20) described this specimen. It has since been freed completely from its matrix and constitutes the basis from which the reconstruction in Fig. 1 was made. In the absence of ANSP 46 (below), ANSP 44 is selected as the replacement neotype.

ANSP 45. Unworn right lower molar (rM_1).

ANSP 46. Large canine. Unlocated, but described in the Academy's catalogue as "?right sabre". This specimen may be the first recognized sabre (Cope, 1880; 1895:240) stated to be in "the Wheatley Collection", and may be the holotype.

ANSP 47. Six isolated specimens comprising: crown of left upper permanent sabre or canine (lC^1); entire left and fragmentary right upper permanent carnassials (P^4's); left upper permanent molar (lM^1); part of a left dentary; and a fragment of bone.

ANSP 48. Eight broken and fragmentary pieces of postcranial skeleton comprising: distal end of left humerus; proximal end of left radius; proximal ends of right metacarpals II and III; small ungual phalanx; entire and damaged right calcanea; and right astragalus.

The specimens on which *Machaerodus (Smilodon) mercerii* Cope, 1899 (= *Smilodontopsis mercerii* [Cope] of Merriam and Stock, 1932) is based comprise:

ANSP 49. Left and right dentaries that articulate to form a single mandible.

ANSP 50. Isolated right lower fourth premolar (rP_4; B.1.4) and left upper third premolar (lP^3; B.3.6), designated as the lectotypes in the catalogue, possibly in Cope's handwriting. These specimens constitute the holotypes of *M. (S.) mercerii*. Three premolars were originally collectively described as *Uncia mercerii* by Cope (1895) but only the two catalogued as ANSP 50 formed the basis for the description of *M. mercerii* in 1899. The third, a right P^4, ANSP 52, probably formed the basis for the identification of *Uncia inexpectata* (= *Crocuta inexpectata,* Cope, 1895; Cope, 1899).

ANSP 51. Thirty-seven bones and fragments of bones, including: distal articulation and part of shaft of ?right humerus; shaft of left metacarpal II; left metacarpals III and V; damaged left metacarpal IV; damaged right metacarpals IV and V; left metatarsal II; damaged left metatarsal V; damaged right metatarsals II, III?, and V; six proximal phalanges; six middle phalanges; and one ungual phalanx.

There appears to be no reliable basis on which elements from one individual or species may be certainly identified. When available elements are assessed to determine the minimum number of individuals from which they could derive, only three are required. The more extensive individual was described as *M. gracilis,* and the less complete individual as *M. mercerii,* although postcranial elements from the two individuals appear to have been mixed. The third individual is represented by the partial left dentary (ANSP 47 partim).

ASPHALTO SPECIMEN

Merriam (1905) described *Machaerodus? ischyrus* on a dentary from Asphalto, Kern County, California, from the western margin of San Joaquin Valley at the foot of the Tremblor Range. This specimen probably derived from the Tulare Beds (Merriam, 1918) and is probably early Blancan (Kurtén and Anderson, 1980). In 1918 Merriam founded the genus *Ischyrosmilus* on this specimen when describing a second species, *Ischyrosmilus idahoensis,* from Froman Ferry, Idaho.

The age of the Asphalto specimen was given as Quaternary or late Pliocene (Merriam, 1905) and Blancan (Mawby, 1965).

The type specimen (UCMP 8140) is a left dentary lacking the coronoid, condyle, and angle, but with well-preserved I_1–I_2, C_1–M_1, and alveolus for I_3.

FROMAN FERRY SPECIMEN

Merriam (1918) described *Ischyrosmilus? idahoensis* on a partial left dentary from Froman Ferry on the Snake River, southwestern Idaho. It was recovered from beds referred to the Idaho Formation at locality 3036C (Museum of Paleontology, University of California) and considered to be of late Pliocene age (Merriam, 1918) or late Blancan faunal age (Kurtén and Anderson, 1980).

The type specimen (UCMP 22343) comprises the ramus of a left dentary, broken obliquely from beneath P_3 to behind M_1, and lacking the genial flange. Roots of all teeth I_1–M_1 are preserved, with parts of the crowns of C_1 and P_3.

RED ROCK CANYON SPECIMEN

Merriam (1919) described *Ischyrosmilus osborni* on a partial dentary from the lower part of the Ricardo Beds in Red Rock Canyon, north of Barstow and west of the El Paso Range, California. He had earlier named it (Merriam, 1918:525) without description or illustration. The age of this specimen was considered early Pliocene by Merriam (1919), but it is Clarendonian, now considered late Miocene at about 10 My ago (Evernden et al., 1964:167).

The type specimen (UCMP 19476) comprises the anterior two-thirds of a left dentary broken posterior to M_1, with I_1–I_3, P_4–M_1, and root of P_3. The alveolus for C_1 is empty and the genial flange is slightly abraded.

Gregory (1942) considered *I. osborni* very similar to *Eusmilus whitfordi* (Barbour and Cook, 1915) and that both were incorrectly assigned generically. He concluded that they were congeneric and probably conspecific, but that paucity of material did not allow the latter conclusion with confidence. He assigned them to "*Megantereon*" sensu lato, but recognized that they were more primitive and could well belong within *Sansanosmilus* or *Albanosmilus*. Kitts (1957) placed Merriam's (1919) *I. osborni* in "*Albanosmilus?*" and Mawby (1965) placed it in "*Sansanosmilus?*" which has the more complete holotype. Schultz, Schultz, and Martin (1970) placed *I. osborni* in their new genus *Barbourofelis* as *B. osborni* on its deep symphysis which is considered a characteristic of the tribe Barbourofelini, and *E. whitfordi* was tentatively placed in the genus as *?Barbourofelis whitfordi* because of a characteristically deep fossa for the superficial masseter and the "long-thin" carnassial, but without detailed discussion. They considered *B. osborni* and *?B. whitfordi* to be Clarendonian (lower part of the Ash Hollow Formation, then middle Pliocene).

Ischyrosmilus osborni thus represents an earlier sabretooth taxon than either the Smilodontini or Homotheriini and belongs within the lineage leading to *Barbourofelis morrisi* of late Clarendonian or early Hemphillian age (middle of the Ash Hollow Formation) and *B. fricki* of "Kimballian" (channel fill above the Ash Hollow Formation) or early Blancan age (Schultz, Schultz, and Martin, 1970).

BROADWATER FORMATION SPECIMENS

Schultz and Martin (1970) described *Ischyrosmilus crusafonti* on a partial left dentary from the Dan Bowman Ranch, 5¼ miles east and ¾ mile north (8 km E and 1.2 km N) of Broadwater, Nebraska. The geological horizon of the specimens is the Lisco Member of the early Pleistocene Broadwater Formation.

The type specimen UNSM 25493 comprises a partial left dentary with I_1–C_1, P_4–M_1, and alveolus for P_3. It is damaged on the genial flanges and broken behind M_1. An isolated left C^1 UNSM 25503 is referred to this species.

Schultz and Martin (1970) also identified *Ischyrosmilus* sp. from the same horizon but 3 miles east and 2 miles north (5 km E and 3 km N) of Lisco, Nebraska. This specimen UNSM 1105 comprises damaged premaxillae with left and right I^2–C^1 and alveoli for I^1's.

CITA CANYON SPECIMENS

Mawby (1965) founded *Ischyrosmilus johnstoni* on 19 cranial and postcranial elements of sabretooths recovered from the Cita Canyon locality, Randall County, Texas (UCMP locality V-3721), of Blancan age. These materials were originally collected for the Panhandle Plains Historical Museum, Canyon, Texas, but five specimens have since been transferred to the Museum of Paleontology, University of California, Berkeley, California.

The specimens assigned to *Ischyrosmilus johnstoni* Mawby, 1965 comprise:

WT 1239 (Type). Mandible with r + lP_4, r + lM_1, lP_3, roots of rC_1 and rP_3. The type is stated to possess "right and left P_4 and M_1, left P_3, roots of left C and P_3, all teeth heavily worn" (Mawby, 1965:576), and his illustration (1965:579, fig. 2) shows the left dentary possessing lP_3–M_1 in alveoli and empty alveoli for lI_1–C_1. Mawby designated the mandible as the type and referred the following specimens to the species:

UCMP 66485. Left maxilla with P^4.

UCMP 66486. Partial right dentary with heavily worn P_4 and M_1.

WT 1025. Upper canine or sabre, C^1 (listed by Mawby as WT 1026).

Fig. 1. *Ischyrosmilus gracilis* (Cope, 1880). Partial reconstructions of the facial and mandibular regions of the sabretooth originally described as *Machaerodus (Smilodon) gracilis* Cope, 1880 from the Port Kennedy Caverns, Pennsylvania, based upon the neotype ANSP 44, with details of the ear region from ROM:B 4733. Only preserved parts are shaded, but probable outlines are restored to complete impressions. Left dentary dotted in A to allow full view of sabre. Scale in centimetres.

A Anterior aspect of facial region.

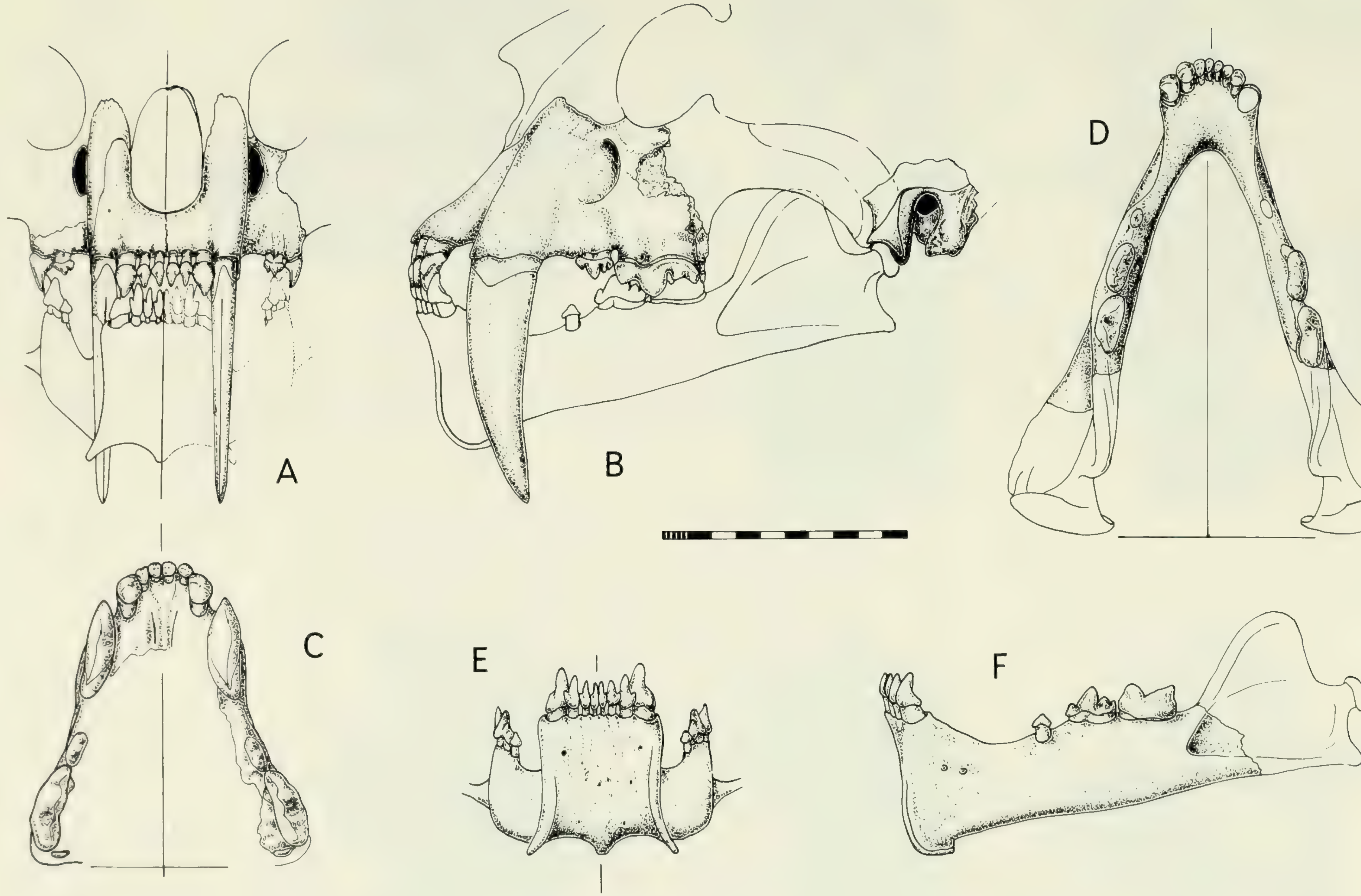
B Left buccal or lateral aspect of facial region with mastoid and glenoid processes and external auditory meatus from ROM:B 4733 from Bass Point Waterway I, Florida.

C Palatal aspect of facial fragment.

D Occlusal aspect of mandible.

E Genial aspect of mandible.

F Buccal or lateral aspect of mandible.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WT 1238. Right dentary fragment with newly worn P_4 and M_1.

WT 1860. Left maxilla with I^1–I^3, P^4 and stump of C^1 and associated damaged braincase.

WT 2615. Left dentary lacking teeth, ?juvenile.

WT 1026, 1528, 1834, and 2429. Fragments of sabres, C^1's.

The following postcranial specimens were considered to be probably referable to *I. johnstoni* by Mawby:

UCMP 66487. Left humerus lacking proximal end.

UCMP 66488. Left femur, lacking distal end and most of greater trochanter.

UCMP 66489. Complete tibia.

WT 625. Right humerus lacking tuberosities and part of caput.

WT 626. Shaft of right femur.

WT 628. Proximal end of right ulna.

WT 1066. Right femur, slightly damaged and distorted.

WT 1691. Distal end of right humerus.

No specimen number. Distal end of left humerus.

Assessment of these specimens for taxonomic homogeneity and for the minimum number of individuals from which the sample could have been derived shows that two taxa and five individuals may be involved. The two taxa comprise a homothere similar to *Homotherium crenatidens* and a smilodont referable to *Ischyrosmilus gracilis,* which are represented by three and two possible individuals, respectively (see Discussion, p. 34).

BASS POINT WATERWAY I SPECIMENS

The area of the site is located in Section 19, Township 39 south, Range 22 east, Town of Northport, Sarasota County, Florida, at latitude 27° north, longitude 82° west.

Many vertebrate fossils were recovered, both *in situ* and in the spoil thrown up in the dredging of the waterway during July and August 1977, and in subsequent years, from the site which is located on the southeast bank of a northeast-southwest trending canal. The site comprises a single *in situ* excavation in the side of the canal bank, about 2 metres below the land surface, and usually below water level. It was first revealed at a time of especially low water. Bones have also been collected from a considerable distance both to the northeast and southwest of the excavation on the bank as they weathered out from the spoil thrown up by the drag-line. At one place at least the sample is heterochronic and comprises a mixture with probable Rancholabrean materials.

The name Bass Point Waterway I (BP I) is reserved for materials excavated *in situ* on three occasions from the site in the southeast bank. Surface-collected specimens are identified as Bass Point Waterway (BP) as they lack geological provenance.

The fossils are hard and black (Figs. 2–7), with most larger elements broken but not widely dispersed. In a few instances rows of associated horse teeth were found in close proximity but lacking any alveolar bone. The specimens derive from a thin layer suggestive of a bone-lag and appear to have been water-sorted, as very little microvertebrate material was obtained by screening the surrounding matrix. The brownish grey matrix immediately enclosing the specimens has not been certainly identified but is likely a fine silt which overlies the surface disconformity of highly aquiferous "barnacle-hash" coquina. This coquina may be the local facies of the Tamiami Formation of probable early Pliocene age. At BP I the fossiliferous horizon is overlaid by a mainly sandy stratum, which appears to extend to the surface and which contains lenses of shells of relatively modern aspect.

The mammalian fauna obtained from BP I is recognized as Blancan (A. G. Edmund, pers. comm.) and includes a chelonian, scimitar cat (*Homotherium*), cat or bobcat (*Felis* or *Lynx*), small equid (*Nannippus phlegon*), zebra (*Equus* [*Dolichohippus*]), small camelid (*Hemiauchenia* or *Palaeolama*), small cervid, and giant armadillo (*Kraglievichia*). All, or almost all, of the Blancan fossils found in the Northport–Port Charlotte area are associated with erosional surfaces of the Tamiami Formation, as far as can be determined, but these surfaces usually lie below the present water-table. The presence of later Rancholabrean fossils, including *Smilodon floridanus,* in the surface sample derived from the drag-line spoil bears evidence to a possible marine transgressional-regressional cycle following the deposition of the Blancan BP I remains.

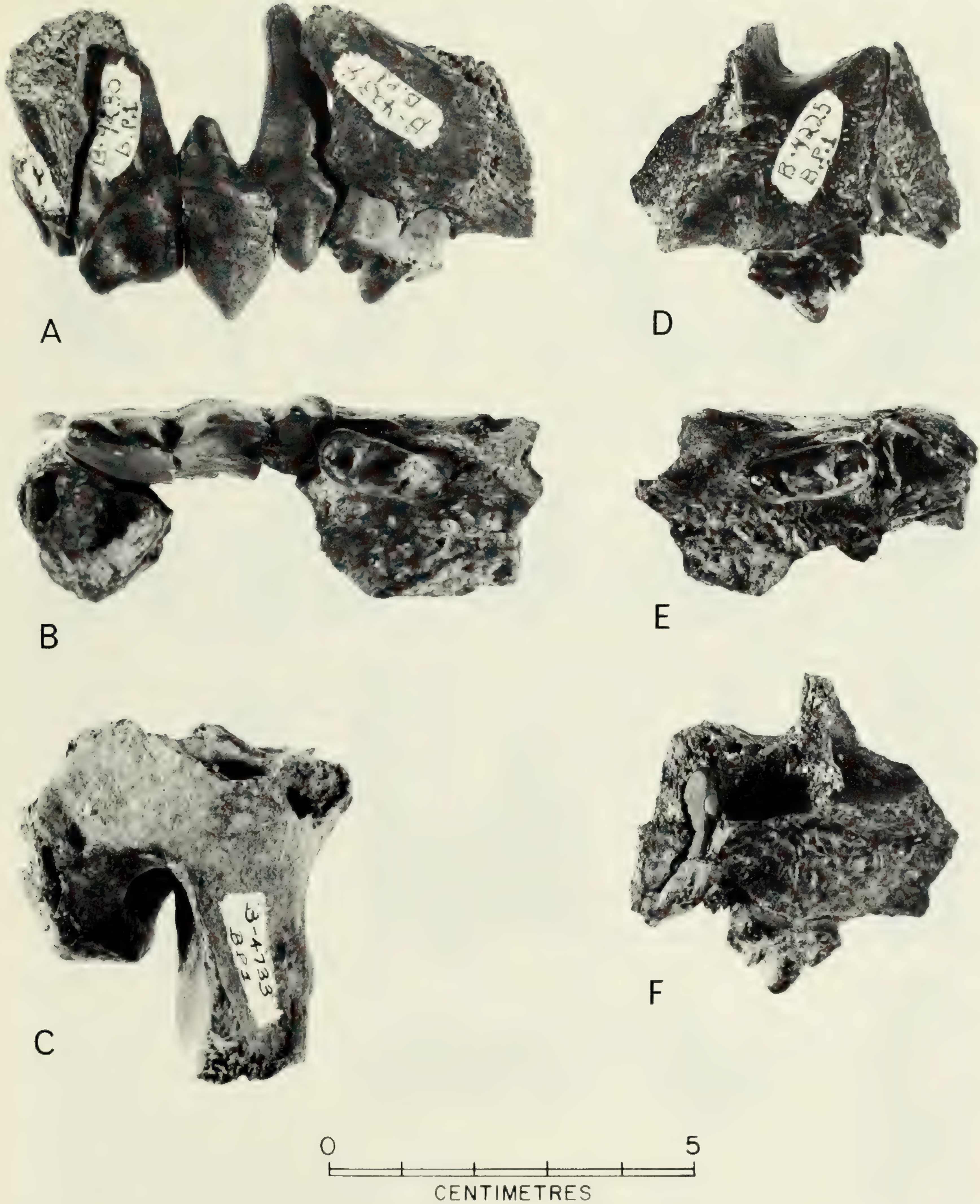
The collections are chiefly in the possession of Mr. William and Mrs. Leila Brayfield, of El Jobean, Florida.

Fig. 2. *Ischyrosmilus gracilis.* Cranial fragments and cheek teeth from Bass Point Waterway I, Florida.

A,B Right maxillary fragments and cheek teeth, rP^3–P^4, (ROM:B 4230, 4234, and 4262). A—buccal or lateral; B—occlusal aspects. Note canine alveolar surface mesially on ROM:B 4234, broken protoradix on ROM:B 4230, and alveolus for M^1 on ROM:B 4262 (behind ROM:B 4230).

C Right glenoid and mastoid processes and external auditory meatus, dorsolateral aspect (ROM:B 4733). Note space between processes leading to the meatus.

D–F Left maxillary fragment with P^3, (ROM:B 4225). D—buccal or lateral; E—occlusal; and F—lingual or medial aspects. Note canine alveolar surface mesially (D, E), ventral margin of infraorbital canal dorsally (D, F), and broken protoradix and pararadix of P^4 distally (D–F).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CENTIMETRES

The elements recovered from BP I duplicate some of the more important elements recovered from the Port Kennedy Caverns, Pennsylvania, and dentaries from Florida and elsewhere, and thus allow significant direct comparisons.

The Bass Point Waterway I sabretooth materials are deposited in the Royal Ontario Museum, Collection of Vertebrate Fossils, and catalogued with the prefix "ROM:B". Selected specimens are illustrated in Figs. 2–7. The materials comprise:

ROM:B 4100. Proximal phalanx, left pes, digit IV; articulates with 4232 (Fig. 6F).

ROM:B 4205. Partially fused premaxillae, with worn stump of eI^2, and alveoli for eI^1, eI^3, and rI^{1-2}.

ROM:B 4225. Left maxillary fragment with P^3, partial alveolar surfaces for C^1 and mesial roots of P^4, and ventral margin of infraorbital canal (Fig. 2D–F).

ROM:B 4228. Right permanent upper canine or sabre, rC^1, central portions of crown and lingual enamel margin only (Fig. 4D).

ROM:B 4229. Right dentary fragment with distal half of fourth premolar, rP_4, and alveoli for first molar or carnassial, rM_1 (Fig. 4N–P).

ROM:B 4230. Right upper permanent fourth premolar or carnassial, rP^4, lacking protocone, protoradix, and mesial half of metacone-hypocone root; paracone root fits well into distal alveolus of 4234 and distal root into alveolus on 4262 (Fig. 2A,B, Fig. 3L–N).

ROM:B 4231. Left permanent upper canine or sabre, lC^1, crown fragment only, lacking distal portion near enamel margin (Fig. 4A,B).

ROM:B 4232. Left metatarsal IV (Fig. 7A–C).

ROM:B 4233. Left metatarsal III, lacking phalangeal articulation (Fig. 6A–D).

ROM:B 4234. Right maxillary fragment with permanent third premolar, rP^3, and alveolar surfaces for root of C^1 and mesial root of P^4; paracone root of 4230 fits well into distal alveolus (Fig. 2A,B).

ROM:B 4235. Right permanent upper third incisor, rI^3 (Fig. 3D–F).

ROM:B 4236. Left permanent lower canine, lC_1 (Fig. 4H–J).

ROM:B 4237. Left permanent upper third incisor, lI^3 (Fig. 3A–C).

ROM:B 4238. Left astragalus, slightly larger in articulation than calcaneum 6007 (Fig. 5A–F).

ROM:B 4249. Left permanent lower second incisor, lI_2 (Fig. 4E–G).

ROM:B 4250. Left permanent lower canine, lC_1, with damaged crown (Fig. 4K–M).

ROM:B 4253. Right maxillary fragment with alveoli for P^3 and alveolar contacts for root of C^1 and pararadix of P^4, and ventral margin of infraorbital canal.

ROM:B 4260. Left maxillary fragment with alveolus for M^1 and alveolar contacts for distal surface of distal root of P^4.

ROM:B 4261. Tip of ?left permanent upper canine or sabre, $?lC^1$ (Fig. 4C).

ROM:B 4262. Right maxillary fragment with alveolus for M^1 and alveolar contacts for distal surface of distal root of P^4 4230 (Fig. 2A, B).

ROM:B 4288. Right permanent upper canine or sabre, rC^1; fragment of crown above enamel margin (Fig. 4D).

ROM:B 4289. Right permanent upper fourth premolar or carnassial, rP^4; distal root and metacone hypocone blade only, worn through to pulp cavity (Fig. 3G, H).

ROM:B 4733. Right glenoid and mastoid processes with external auditory meatus (Figs. 1B, 2C).

ROM:B 4734. Right premaxillary fragment with alveolar surfaces for roots of I^3 and C^1; root of 4235 fits well into incisive alveolus.

ROM:B 4735. Right maxillary fragment with alveoli for distal root of P^4 and root of M^1; distal root of 4230 fits well into alveolus for distal root of P^4 (Fig. 2A,B).

ROM:B 6007. Left calcaneum; see 4238 (Fig. 5G–J).

ROM:B 6037. First or proximal phalanx, ph. I, of digit I, right manus (Fig. 7E).

ROM:B 6084. Left permanent upper fourth premolar or carnassial, lP^4, mesial half only; split through metacone near protocone (Fig. 3O–R).

ROM:B 6088. Left permanent upper third premolar, lP^3 (Fig. 3I–K).

ROM:B 6574. Right metatarsal III, lacking phalangeal articulation (Fig. 6E–H).

Fig. 3. *Ischyrosmilus gracilis*. Isolated upper incisors and cheek teeth from Bass Point Waterway I, Florida.

A–C Left permanent upper third incisor, lI^3, (ROM:B 4237). A—lateral or distal; B—lingual; and C—medial or mesial aspects.

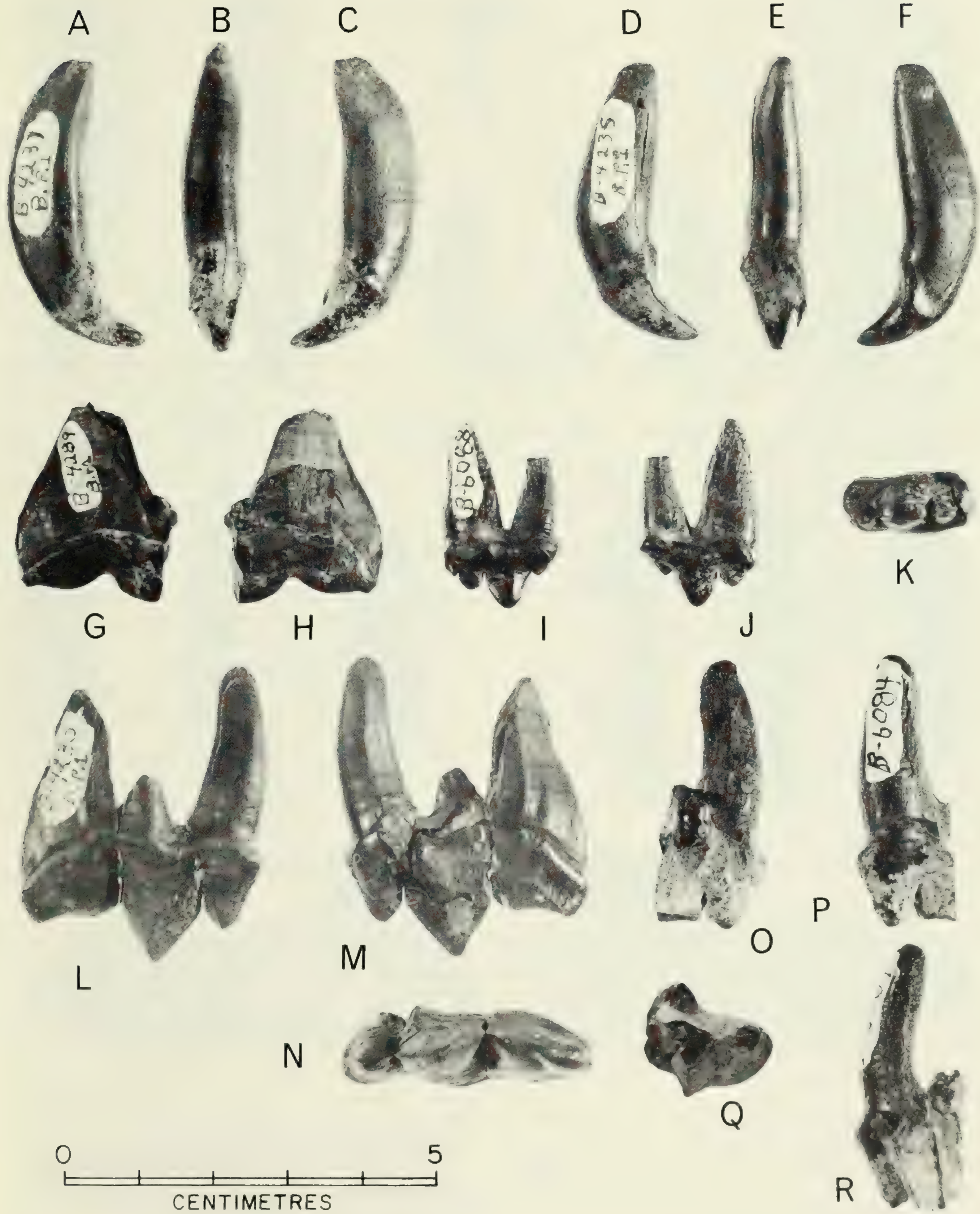
D–F Right permanent upper third incisor, rI^3, (ROM:B 4235). D—medial or mesial; E—lingual; and F—lateral or distal aspects.

G, H Right permanent upper fourth premolar or carnassial, rP^4, distal root and crown fragment, (ROM:B 4289). G—lateral or buccal; and H—medial or lingual aspects. Note worn shear surface and exposed pulp cavities in H.

I–K Left permanent upper third premolar, lP^3, with broken mesial root, (ROM:B 6088). I—lingual or medial; J—buccal or lateral; and K—occlusal aspects.

L–N Right permanent upper fourth premolar or carnassial, rP^4, with broken protoradix, (ROM:B 4230). L—buccal or lateral; M—lingual or medial; and N—occlusal aspects.

O–R Left permanent upper fourth premolar or carnassial, lP^4, paracone and root, (ROM:B 6084). O—lingual or medial; P—buccal or lateral; Q—occlusal; and R—distal or posterior aspects. Note evidence of protoradix in O, Q, and R.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CENTIMETRES

The minimum number of individuals from which this sample could be derived is two, one of which was aged and the other a young adult. The aged individual possessed well-worn carnassials and is catalogued as ROM:B 4289, with possibly 4228, 4234, 4250, 4253, and 4261. The young adult is represented by the other cranial specimens and is identified by the lack of wear on the shearing surfaces of the carnassials 4230 and 6084 and on the canine tips. The glenoid and auditory meatus specimen 4733 may derive from either individual, as may the pedal elements. The astragalus 4238 and calcaneum 6007 fit together imperfectly and may represent either the older and younger animals, respectively, or an individual with more tolerance between the facets of the two elements.

The Bass Point Waterway collection is composed of black, well-mineralized specimens which preserve small features and show no effects of weathering or rounding by water although many have been broken before deposition or during recovery.

The Bass Point specimens include parts of upper and lower dentitions, partial dentaries, astragalus, and metatarsal III, which are comparable to those of the Port Kennedy *M. gracilis* discovery and from which they do not differ markedly either in detail or size. The upper canine (4228) is more gracile (perhaps indicating individual, sexual, or regional variation), and P^3 (4225, 4234) is longer, probably reflecting variation intrinsic to this tooth.

EL JOBEAN PIT SPECIMEN

An isolated left maxilla (B 8400) with third and fourth premolars, lP^3–P^4, was recovered from El Jobean Pit, Charlotte County, Florida, by Mr. and Mrs. William Brayfield in August 1982. The El Jobean Pit is located in Section 21, Township 40, Range 21 East, Charlotte County at approximately latitude 27° north, longitude 82° west, and is an operating gravel pit.

The specimen was found in a black sand and green silt member similar to that from which the Bass Point Waterway I specimens derived and which, in the El Jobean Pit, overlies the Caloosahatchee Shell Beds. Associated faunal elements comprise a gomphothere proboscidean (*Cuvieronius?*), small equid (*Nannippus phlegon*), and giant armadillo (*Holmesina floridanus*), indicating a Blancan age (W. Brayfield and A. G. Edmund, pers. comm., 1982).

The specimen (Brayfields' Collection B 8400: Fig. 8) comprises most of a left maxilla in which the palatal shelf at the level of P^3 and alveolar margins of the canine alveolus are damaged. The premolars, P^3 and P^4, are nearly undamaged, although both are worn, especially P^4. Alveoli for C^1 and M^1 are preserved. Sutural contacts with the premaxilla, frontal and palatine, are preserved, and the anterior buttress of the jugal is present to preserve the inferior margin of the orbit and the base of the zygomatic arch.

The individual from which B 8400 derived was old or very mature from the worn state of P^4, which correlates with the fused condition of the anterior root of the jugal. The carnassial P^4 lacks a protocone but has a protoradix (Fig. 8D). P^4 and P^3 have a small distolingual wear facet. Both premolars show a vertically striated pattern of wear different from that in the Bass Point Waterway I specimens (Fig. 3G–R). M^1 was triangular in section and presumably styliform. The facial aperture of the infraorbital canal is deep and wide, as in the type *M. gracilis* (Fig. 1A,B) and in smilodonts, but in lateral aspects the lateral margin is less curved and nearly vertical.

SANTE FE RIVER I SPECIMEN

An isolated lower fourth premolar (rP_4, FDT 488) was recovered from Santa Fe River locality I, in Gilchrist and Columbia counties, Florida (Webb, 1974). Kurtén (1965:220) suggested that this site is heterochronic, with many fossils "undoubtedly Late Pleistocene" while "others may be as old as the Blancan" and some of the felid materials "might be middle Pleistocene in age". Kurtén (1965:241, fig. 14 Above) illustrated the tooth and dated it as "probably Middle Pleistocene". Webb (1974:150) agreed with Kurtén, dated the river site as

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Fig. 4. *Ischyrosmilus gracilis*. Isolated upper canine or sabre fragments, lower incisors, and fragment of dentary from Bass Point Waterway I, Florida.

A,B Left permanent upper canine or sabre, lC^1, crown fragment, (ROM:B 4231). A—lingual; and B—buccal aspects.

C ?Left permanent upper canine or sabre, lC^1, tip, (ROM:B 4261).

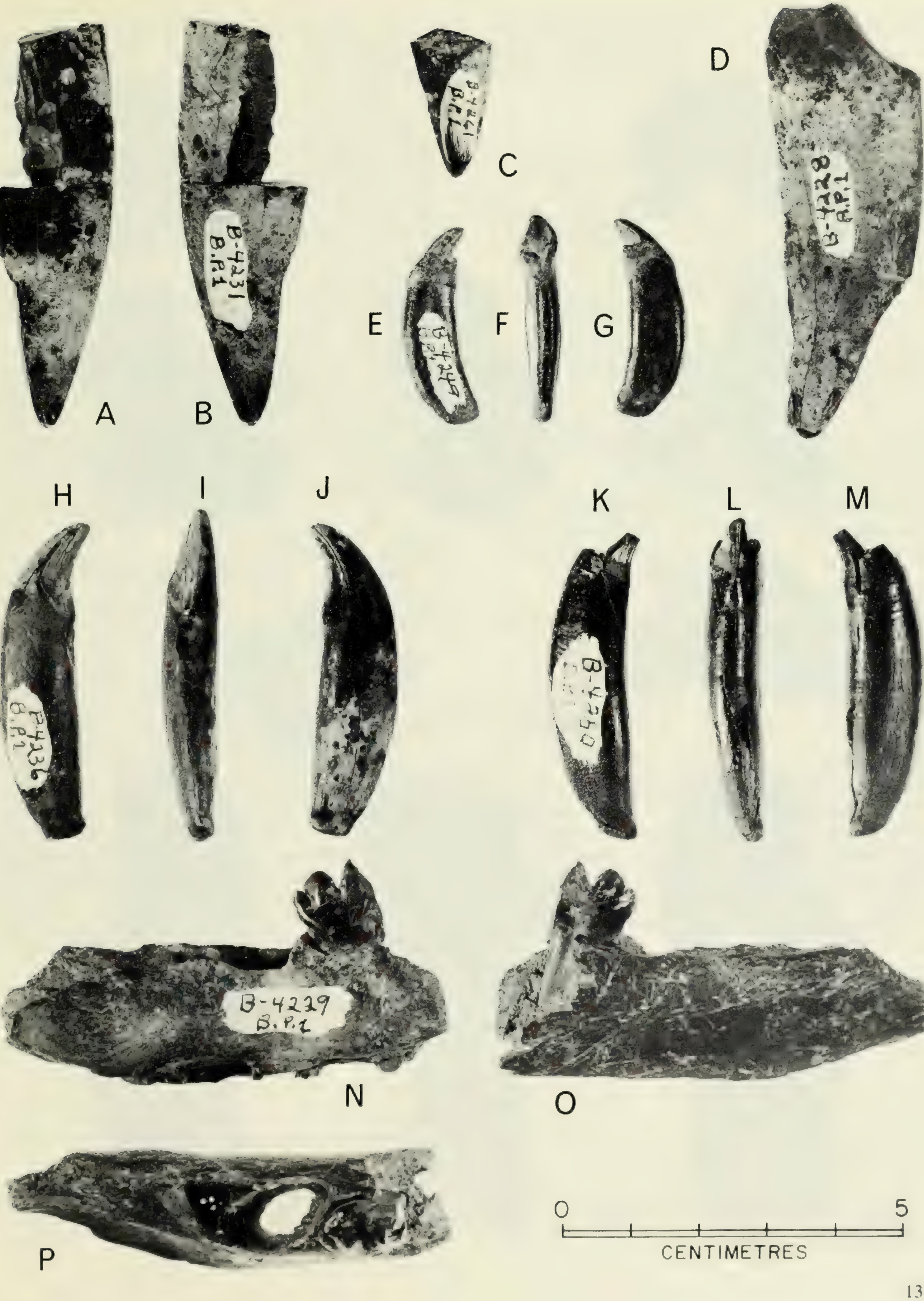
D Right permanent upper canine or sabre, rC^1, basal portion of crown, (ROM:B 4228). Buccal aspect.

E–G Left permanent lower second incisor, lI_2, (ROM:B 4249). E—lateral or distal; F—lingual; and G—medial or mesial aspects.

H–J Left permanent lower canine, lC_1, (ROM:B 4236). H—lateral or buccal; I—lingual or posterior; and J—medial or mesial aspects.

K–M Left permanent lower canine, lC_1, with damaged crown, (ROM:B 4250). K—lateral or buccal; L—lingual or posterior; and M—medial or mesial aspects.

N–P Right dentary fragment with distal half of P_4 and alveoli for M_1, (ROM:B 4229). N—buccal or lateral; O—lingual or medial; and P—occlusal aspects. Note root of P_4 in N protruding below the ventral boundary.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"late Blancan", and assigned the specimen to *Smilodon gracilis* Cope although Kurtén had assigned the tooth to "*Smilodon* sp., possibly *Smilodon fatalis* or *Smilodon gracilis*".

INGLIS IA SPECIMENS

Inglis Locality IA is located in Citrus County, Florida, and yields an early Irvingtonian fauna (Klein, 1971; Webb, 1974; Kurtén and Anderson, 1980). The sabretooth remains include cranial, dental, and postcranial elements of gracile form. The materials are deposited in the Florida State Museum, University of Florida, Gainesville, Florida, and have been described by Annalisa Berta (pers. comm., 1982). I examined casts of a right dentary (UF 20065), and these show a permanent fourth premolar and first molar (P_4–M_1), the alveolus for P_3, partial alveoli for I_3–C_1, and the symphysis and genial flange, but lack the coronoid, condyle, and angle. This small machairodont was referred to *Smilodon gracilis* by Klein (1971), Webb (1974), Kurtén and Anderson (1980), and A. Berta (pers. comm., 1982). The cast almost matches in its preserved areas the left dentary from Port Kennedy Caverns and is comparable with the dentaries assigned to *Ischyrosmilus* by Merriam (1905, 1918, 1919) and Mawby (1965).

HAILE XVA SPECIMENS

The Haile XVA sabretooth specimens form part of a Blancan fauna (Webb, 1974) of latest Pliocene age (Robertson, 1976) recovered from a fissure in Ocala (Eocene) limestone near Haile, Alachua County, Florida. The specimens comprise the distal end of a right tibia and a right astragalus (UF 17496, jointly catalogued), which articulate well together, and a right metacarpal II (UF 17498), which are presumed to derive from a single individual (Robertson, 1976). Robertson (1976:157) referred the specimens to *Smilodon* because of "(1) the presence of the astragalar foramen; and (2) the medial facet for the calcaneum and facet for the navicular are merged". The fusion of the navicular and medial calcanear facets was also observed by Merriam and Stock (1932).

These specimens are not directly comparable to the other described Florida materials, although the astragalus may be compared to that from Bass Point Waterway I and to astragalus ANSP 48 from Port Kennedy Caverns which was described by Cope (1880) as *Machaerodus (Smilodon) mercerii*. Webb (1974) and Robertson (1976) assigned these specimens to *Smilodon gracilis*.

OTHER SPECIMENS

A. Berta (pers. comm., 1982) reported and described additional specimens from El Jobean, Inglis IA, and McLeod A.

Systematic Discussion

SYNONYMY

Familiarity with names of the North American Pliocene and Pleistocene sabretoothed cats is insufficient for the nomenclature and taxonomy to be clear, as names have been misspelled and distinctions between members of the tribes Smilodontini and Homotheriini ignored or confused. The following synonymy presumes the conclusions that will become evident at the end of this discussion and is inserted here for the benefit of readers. The synonymy is limited to selected North American taxa or taxa that were present in North America, although other Eurasian and South American taxa may have had representatives in North America. Each taxon is cited with its synonyms and with geographical localities or distribution.

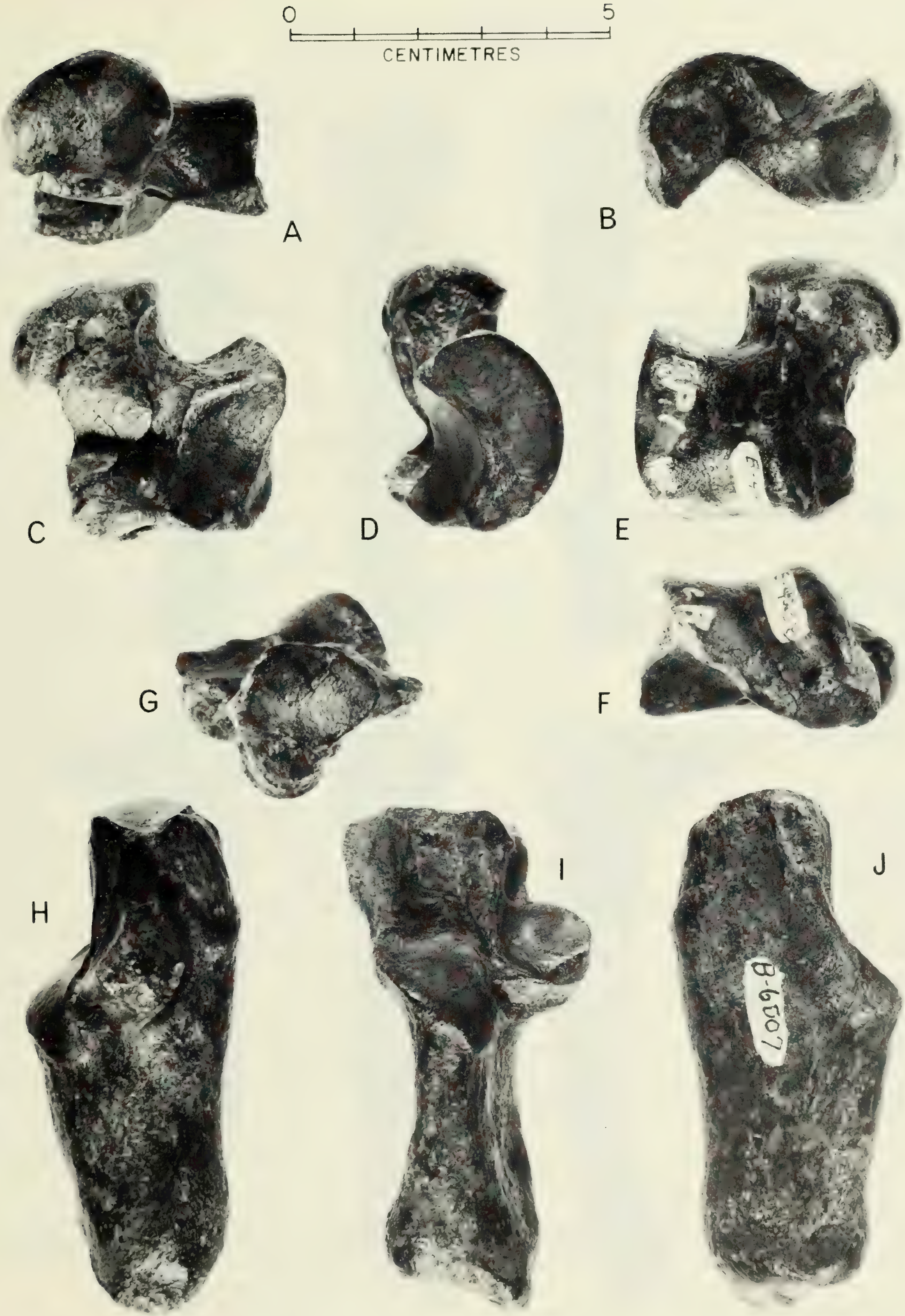
Family Felidae Gray, 1821:302 (includes Machaerodontidae Woodward, 1898:399)
Eurasia, Africa, North and South America

Subfamily Machairodontinae Gill, 1872:59
Eurasia, Africa, North and South America

Fig. 5. *Ischyrosmilus gracilis*. Astragalus and calcaneum from Bass Point Waterway I, Florida.

A–F Left astragalus, (ROM:B 4238). A—distal or navicular; B—medial; C—ventral or calcanear; D—lateral; E—proximal or tibial; and F—posteroproximal aspects.

G–J Left calcaneum, (ROM:B 6007). G—distal or cuboid; H—medial or sustentacular; I—dorsal or astragalar; and J—lateral aspects.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Tribe Homotheriini Kurtén, 1963:97
Eurasia, Africa, and North America

Genus *Homotherium* Fabrini, 1890:176
Eurasia, Africa, and North America

Machairodus—Fabrini, 1890:175, Val d'Arno, Italy.
Dinobastis Cope, 1893:896, Western Oklahoma.
Epimachairodus—Simpson, 1945:120, Eurasia.
Smilodon—Hibbard, 1952:12, McPherson, Kansas.
Ischyrosmilus?—Kurtén, 1963:98, America.

Species *Homotherium serum* (Cope, 1893)
North America

Dinobastis serus Cope, 1893:896, Western Oklahoma.
Homotherium serum—Churcher, 1966:272: Friesenhahn Cave, Texas; Hamman Pit, Kansas. Rawn-Schatzinger and Collins, 1981:18: Old Crow Basin, and Dawson, Yukon; American Falls Lake Beds, Idaho; San Francisco Bay, California; Delmont, South Dakota; Sand Draw, Nebraska; Sandahl, and McPherson, Kansas; Hennesey, Oklahoma; Slaton, Bagett Cave, Gilliland, Laubach Cave, and Friesenhahn Cave, Texas; Gassaway Fissure, Tennessee; Reddick IA and Inglis IA, Florida.
?Ischyrosmilus johnstoni Mawby, 1965:573 partim, Cita Canyon, Texas.

Tribe Smilodontini Kurtén, 1963:97
Eurasia, Africa, North and South America

Genus *Ischyrosmilus* Merriam, 1918:524
North America

Ischyrosmilus Merriam, 1915:262 nomen vanum, Ricardo, California.
Ischyrosmilus Merriam, 1917:425, 430 nomen vanum, Tulare, California.

Species *Ischyrosmilus gracilis* (Cope, 1880)
North America

Machaerodus (Smilodon) gracilis Cope, 1880:857, Port Kennedy Caverns, Pennsylvania.
Uncia mercerii Cope, 1895:392 partim, Port Kennedy Caverns, Pennsylvania.
Smilodon gracilis—Cope, 1895:448, Port Kennedy Caverns, Pennsylvania.
Machaerodus (Smilodon) mercerii—Cope, 1899:240, Port Kennedy Caverns, Pennsylvania.
Machaerodus? ischyrus Merriam, 1905:173, Asphalto, California.
Smilodontopsis (Machaerodus) gracilis—Brown, 1908:191, Port Kennedy Caverns, Pennsylvania.
Smilodontopsis (Machaerodus) mercerii—Brown, 1908:191, Port Kennedy Caverns, Pennsylvania.
Dinobastis (Machaerodus) ischyrus—Brown, 1908:191, Asphalto, California.
?Ischyrosmilus ischyrus Merriam, 1917:425 nomen vanum, McKittrick, California.
Ischyrosmilus? idahoensis Merriam, 1918:524, Froman Ferry, Idaho.
Ischyrosmilus ischyrus Merriam, 1918:524, McKittrick, California.
Machaerodus? gracilis—Matthew, 1918:229, Port Kennedy Caverns, Pennsylvania.
Machaerodus? mercerii—Matthew, 1918:229, Port Kennedy Caverns, Pennsylvania.
Smilodon (Smilodontopsis) gracilis—Merriam and Stock, 1932:15, Port Kennedy Caverns, Pennsylvania.
Smilodon (Smilodontopsis) mercerii—Merriam and Stock, 1932:15, Port Kennedy Caverns, Pennsylvania.
Machaerodus gracilis—Slaughter, 1960:490, Port Kennedy Caverns, Pennsylvania.
Ischyrosmilus johnstoni Mawby, 1965:583 partim, Cita Canyon, Texas.
Ischyrosmilus crusafonti Schultz and Martin, 1970:34, Broadwater, Nebraska.
M(eganterion) gracilus Martin, 1980:149, no referred material.

Fig. 6. *Ischyrosmilus gracilis*. Metatarsals III from Bass Point Waterway I, Florida.

A–D Left third metatarsal, mt. III, lacking phalangeal or distal articulation, (ROM:B 4233). A—medial or internal; B—dorsal or anterior; C—lateral or external; and D—proximal or cuneiform aspects.

E–H Right third metatarsal, mt. III, lacking phalangeal or distal articulation, (ROM:B 6574). E—medial or internal; F—dorsal or anterior; G—lateral or external; and H—proximal or cuneiform aspects. Note puncture, marks of gnawing, and abrasions on dorsal surface seen in F and G.


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Genus *Smilodon* Lund, 1842:193
North and South America

Felis—Leidy, 1868:175, Hardin County, Texas.
Trucifelis Leidy, 1868:175, Hardin County, Texas.
Machaerodus—Lydekker, 1884:33, Hardin County, Texas.
Drepanodon—Leidy, 1889:14, Ocala, Marion County, Florida.
Machairodus—Leidy, 1889:14, Ocala, Marion County, Florida.
Smilodontopsis Brown, 1908:188, Conard Fissure, Arkansas.

Species *Smilodon fatalis* (Leidy, 1868)
North America

Felis (Trucifelis) fatalis Leidy, 1868:175, Hardin County, Texas.
Trucifelis fatalis Leidy, 1868:175, Hardin County, Texas.
Machaerodus fatalis—Lydekker, 1884:333, Hardin County, Texas.
Drepanodon or *Machairodus floridanus* Leidy, 1889:14, Ocala, Marion County, Florida.
Smilodon floridanus—Adams, 1896:433, Ocala, Marion County, Florida.
Smilodon californicus Bovard, 1907:155, Rancho La Brea, California.
Smilodontopsis troglodytes Brown, 1908:188, Conard Fissure, Arkansas.
Smilodontopsis conardi Brown, 1908:190, Conard Fissure, Arkansas.
Smilodon nebrascensis Matthew, 1918:228, Hay Springs Quarry, Sheridan County, Nebraska.
Smilodon (Trucifelis) californicus—Merriam and Stock, 1932:16, Rancho La Brea, California.
Smilodon (Trucifelis) fatalis—Merriam and Stock, 1932:16, Hardin County, Texas.
Smilodon (Trucifelis) floridanus—Merriam and Stock, 1932:16, Ocala, Marion County, Florida.
Smilodon (Trucifelis) californicus—Merriam and Stock, 1932:16, Ocala, Marion County, Florida.
Smilodon (Trucifelis) nebrascensis—Merriam and Stock, 1932:16, Hay Spring Quarry, Sheridan County, Nebraska.
Smilodon (Trucifelis) californicus brevipes Merriam and Stock, 1932:161, Rancho La Brea, California.
Smilodon trinitiensis Slaughter, 1960:487, Trinity River, Second Terrace, Dallas, Texas.

COMPARISONS OF BROWN'S (1908) *SMILODONTOPSIS TROGLODYTES* AND *S. CONARDI* WITH *SMILODON*

When the various specimens assigned to *Smilodontopsis troglodytes*, *S. conardi*, and *Smilodon* sp. from the Conard Fissure are compared with each other, no obviously distinctive differences are apparent among comparable elements. Measurements of the dental elements fall within the recorded size ranges available for *Smilodon* from Rancho La Brea, California, and Talara, Peru (Table 1). Merriam and Stock (1932:13) remarked on the presence of single-rooted P_3's in both individuals of the Conard *Smilodontopsis* since such teeth occur in only 6 per cent of *S. californicus*. They suggested that this tooth "was more frequently developed in the Arkansas form than in the type from California. Moreover, its presence may have been typical in *Smilodontopsis*." They also said the teeth in the Conard specimens showed less reduction than in *S. californicus*, and Brown (1908:190) stated "P_3 is single rooted and oval in outline, with the internal face flattened; the apex of the cone above the base of the crown, inside measurement, is equal to the transverse measurement of the tooth at this point; there is a distinct anterior basal cone about half the size of the posterior basal cone. Two other separate teeth, p^3, show the same characters." Merriam and Stock (1932) considered that P_3 of *Smilodon californicus* is not of this type, all the cusps being reduced, and concluded that *Smilodontopsis* appeared to be more primitive than the species from Rancho La Brea. However, my examinations of P_3's of *S. californicus* indicate that examples matching the size and development of specimens ascribed to *Smilodontopsis troglodytes* and *S. conardi* are present, and consequently Merriam and Stock's conclusion is not generally supportable.

Merriam and Stock (1932) considered that the postcranial elements assigned to *Smilodontopsis conardi* resembled those from Rancho La Brea. They stated (1932:14) that the scapholunar "is of relatively small size but resembles more closely in structure the comparable element in [*Smilodon*] than in true cats," but that "the palmar border of the surface of the magnum does not show the characteristic notch seen in specimens from. . ." Rancho La Brea. Measurements of the metapodials lie at the lower end of the range of variation for metapodials of *S. californicus* but are larger than those referred to *Smilodon c. brevipes* by Merriam and Stock (see Table 2).

Merriam and Stock (1932:14) concluded that "all the characters, with one exception, which Brown (1908:188) regarded as generically distinctive of *Smilodontopsis* are found to apply equally well to *Smilodon californicus*. The single exception, namely the presence and character of $P^{\bar{3}}$, has already been commented upon." This exception, as discussed above, is not valid, and matching examples are present in the Rancho La Brea population of *S. californicus*. Kurtén and Anderson (1980) list both *Smilodontopsis troglodytes* and *S. conardi* as junior synonyms of *Smilodon fatalis*.

When measurements of the various elements originally attributed to *Smilodontopsis troglodytes* and *S. conardi* are

Fig. 7. *Ischyrosmilus gracilis*. Metatarsals IV and phalanges from Bass Point Waterway I, Florida.

A–D Left fourth metatarsal, mt. IV, (ROM:B 4232). A—medial or internal; B—dorsal or anterior; C—lateral or external; and D—proximal or cuneiform aspects.

E Proximal or first phalanx, ph. I, of digit I, right manus, (ROM:B 6037). Dorsal or anterior aspect.

F Proximal or first phalanx, ph. I, probably from digit IV, left pes (ROM:B 4100). Dorsal or anterior aspect. Articulates with ROM:B 4232.

compared (Table 2), no distinctions are evident beyond normal variation within a population. Because no quantitative or qualitative basis exists that distinguishes the Conard Fissure sabretooth material at the specific or higher taxonomic level, all specimens, whether described as *Smilodontopsis* or *Smilodon?*, can be placed in a single species. When these specimens are compared with similar elements from Rancho La Brea, they are again indistinguishable on qualitative or quantitative criteria.

The Conard sabretooth is thus properly referred to *Smilodon* Lund, 1842 and, as the Fissure's deposits are Pleistocene (and their age cannot be determined more accurately), and the animal indistinguishable from *S. californicus*, assignment to the species *S. fatalis* (Leidy, 1868), *S. floridanus* Leidy, 1889, and *S. californicus* Bovard, 1907 must be considered. Slaughter (1963) and Kurtén (1965) considered *S. fatalis* to have existed during Illinoian, Sangamon, and early Wisconsin times and *S. floridanus* and *S. californicus* during late Wisconsin and possibly early Holocene times. Kurtén (1965) postulated

that *S. floridanus* might include *S. californicus*, and Webb (1974) confirmed their single identity. Webb also noted that *S. floridanus* was recovered from Sangamon deposits at Arredondo IA in Florida. Kurtén and Anderson (1980) placed *Smilodontopsis troglodytes* and *S. conardi* within *Smilodon fatalis*. Thus the Conard Fissure *Smilodon* may be referred to *S. fatalis* (Leidy, 1868) which, in its turn, may be the senior synonym of *S. floridanus* Leidy, 1889 when more extensive samples of the Illinoian populations are available. The genus *Smilodontopsis* Brown, 1908 is thus a junior synonym of *Smilodon* Lund, 1842, and the species *troglodytes* Brown, 1908 and *conardi* Brown, 1908 are junior synonyms of *floridanus* Leidy, 1889, in which is also included *californicus* Bovard, 1907.

COMPARISONS OF COPE'S (1880, 1899) *MACHAERODUS (SMILODON) GRACILIS* AND *M. (S.) MERCERII* WITH *SMILODON*

Machaerodus (Smilodon) gracilis and *M. (S.) mercerii* were originally described by Cope (1880, 1895, 1899) on material derived from Port Kennedy Caverns, Pennsylvania. This material probably represents remnants from three individuals, and it is again arguable whether three individuals associated in a single deposit could derive from two nearly identical species. Merriam and Stock (1932) questioned the validity of Cope's specific distinction but did not propose that *M. (S.) mercerii* was conspecific and synonymous with *M. (S.) gracilis*. However, they did consider that these species were definitely distinct from *Smilodon (Smilodon) californicus* and assigned the two species to the subgenus *Smilodontopsis* rather than the subgenus *Smilodon* to emphasize the divergence from the latter and a probable closer affinity to the Conard Fissure sabretooth.

As shown above, the genus *Smilodontopsis* Brown, 1908 is based on *Smilodontopsis troglodytes* (and *Smilodontopsis conardi*), which are conspecific with *Smilodon floridanus*, and thus *Smilodontopsis* Brown, 1908 is a junior synonym of *Smilodon* Lund, 1842. As *Machaerodus gracilis* and *M. mercerii* differ markedly from *Smilodon* both morphologically and temporally, they must be considered separately for assignment to generic or subgeneric taxa.

Merriam and Stock (1932:15) gave the main characteristics of *M. gracilis* and *M. mercerii* as the presence of P_3, the greater "inferior development of the forward flange of the mandible," a noticeably smaller C_1 which is only slightly more massive than I_3, and a slenderer sabre. They suggested that the presence of P_3 and the smaller C_1 indicate affinity to *Smilodontopsis* Brown (= *Smilodon* Lund) and possibly to *Dinobastis* Cope (= *Homotherium* Fabrini) as C_1 is always heavier than I_3 in *Smilodon californicus*. Churcher (1966) showed that North American *Dinobastis serus* Cope, 1893 was distinct from *Smilodon* and congeneric with *Homotherium* Fabrini, 1890 as *Homotherium serum* (Cope, 1893), and that the closest affinity is to the Chinese *H. ultimum* from the Villafranchian of Locality 9 at Choukoutien.

Examination of the specimens referred to as *Machaerodus gracilis* and *M. mercerii* show that they bear little resemblance to those described as *Smilodon troglodytes* and *S. conardi* (i.e., *Smilodon floridanus*) and in fact differ markedly from the general suite of characters that distinguish *Smilodon* and with which the Conard Fissure materials agree. Thus the use of *Smilodon* as a subgenus for the Port Kennedy sabretooth, as originally suggested by Cope (1880, 1899), may be unwarranted.

The facial region and mandibles of *M. gracilis* and *M. mercerii* are more slender and more lightly built than are those of *S. troglodytes* (including *S. conardi* = *S. floridanus*: Fig. 1, Table 3). The sabre (Fig. 9C) is more gracile, proportionately shorter, and with the serrations on the margins differing in quality and degree. The serrations in *M. gracilis* are less beadlike and extend relatively farther across the distal faces of the tooth, whereas those of *Smilodon* are more rounded and are restricted to the mesial and distal margins of the sabres. Serrations are present on the distal margin but are nearly absent on the mesial in both taxa, and are finer in *M. gracilis* or *M. mercerii*, where they are smaller. Serrations are absent from all other teeth except C_1.

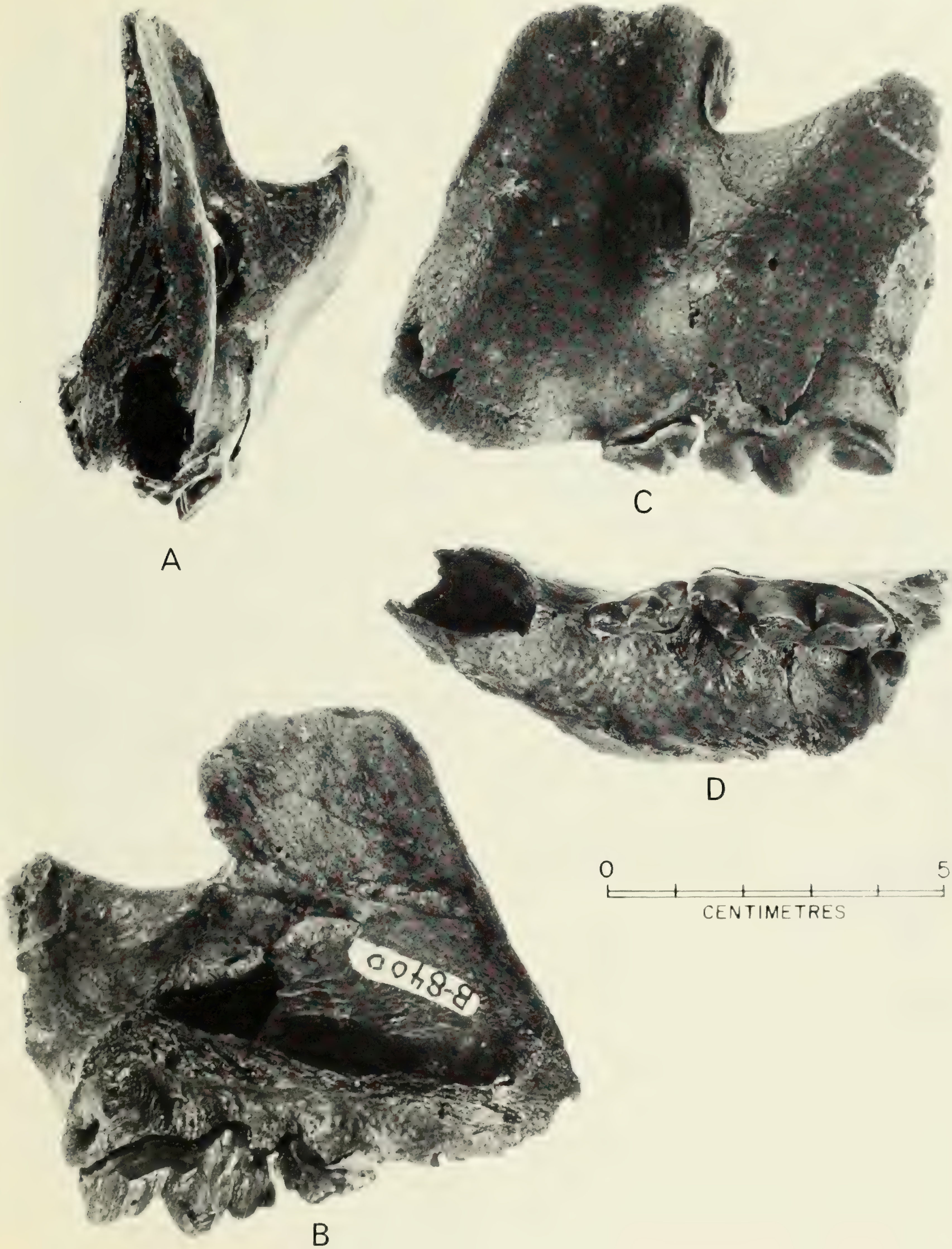
Four well-developed cusps on P^3 correspond to the parastyle, paracone, metacone, and buccodistal style of P^3 in *Smilodon*. However, these cusps show little or no reduction, although the tooth is low crowned, and thus cannot be considered to match the condition of P^3's in *Smilodon*.

The upper carnassial, P^4, lacks the lingual protocone but has a well-developed protoradix. The paraconule is large and usually lacks a mesial ectoparastyle.

The mandible is smaller in all dimensions in *M. gracilis*

Fig. 8. *Ischyrosmilus gracilis*. Partial left maxilla with third and fourth premolars, P^3–P^4, (ROM:B 8400), from El Jobean Pit, Florida. Compare B 8400 with neotype of *M. gracilis* (Fig. 1A–C) and premolars with those from Bass Point Waterway I (Fig. 2A,B,D–F, Fig. 3G–R).

A–D A—anterior; B—medial; C—buccal or lateral; and D—palatal aspects.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CENTIMETRES

than in *Smilodon* (Table 4), and the mental or genial flanges of the chin are thinner and extend ventrally well beyond the margin of the ramus, a development that is absent in all known specimens of *Smilodon* (Fig. 10B,C). The mental foramina are double, and two or three accessory foramina may occur medial to the genial flanges. The condition of these foramina varies in *Smilodon*, but a single mental foramen is usual although double foramina occur in the Talara, Peru, and Californian populations of *Smilodon*, and the anterior accessory foramina vary in number from two to five. The jaws are less robust and thinner buccolingually than in *Smilodon* and in morphology greatly resemble some of the earlier sabretoothed carnivores (e.g., *Hoplophoneus, Dinictis, Machairodus*, or *Megantereon*).

The dentition as a whole is smaller and less massive than in *Smilodon* and readily distinguishes the two taxa. The lower canine, C_1, is serrated on the distal margin of the crown as in the sabres and P^4 is higher crowned but with cusps that are not as elongate nor as slanted distally.

When measurements of the preserved cranial elements of *M. gracilis* and *M. mercerii* are compared with the observed ranges of variation for measurements of similar elements of *Smilodon* from Rancho La Brea and Talara, overlaps occur only in the lower range of 10 of 36 dimensions and are indicated by asterisked superscript indices (Table 3). Characters 1–3 involve the length of upper diastema, a dimension that is highly variable in many mammals, as it is dependent on size and age and degree of maturation of the individual. Characters 4, 5, 7, and 10 involve the mesiodistal diameters of I^1, P^3, P^4, and M^1. The three teeth I^1, P^3, and M^1 are relatively small and variable in size as they are undergoing reduction in *Smilodon*. Character 7 (mesiodistal diameter of P^4) is dependent on the development of the mesial parastyle (Character 8) which may or may not be present, and is functionally interrelated to Character 5 (mesiodistal diameter of P^3) in the provision of a shearing blade. The presence of a parastyle on P^4 usually correlates with a smaller P^3 in *Smilodon*. Character 6 (crown height at protocone of P^3) reflects the development of the shearing function on P^4, with smaller protocones on P^3 correlating with greater carnassialization of P^4. In Character 9 (metacone blade length of P^4) all of the measurements for *M. gracilis* lie within the lower part of the size range for P^4's of *Smilodon* and reflect the gracile form of the former sabretooth. Characters 8, 9, and 10 (dimensions of the crown of M^1) reflect the small size and variability inherent in a tooth that has undergone reduction and is variable in all Felidae, and overlapping measurements are expected in taxa of similar size. Most of the overlaps at the lower extremes of the size ranges indicate that the Port Kennedy sabretooths had a dentition that was about the same size as that of the smaller individuals of *Smilodon* from the late Pleistocene of Rancho La Brea and Talara.

Table 4 gives measurements of the mandible and lower dentition of the Port Kennedy sabretooths compared with specimens referred to as *Smilodon gracilis* from Florida and ranges of variation in *Smilodon* from Rancho La Brea and Talara. Overlaps in the ranges of variation for the Port Kennedy sabretooths' dimensions with those of *Smilodon* from Rancho La Brea and Talara occur in 13 of 47 dimensions measured and are indicated by asterisked superscript indices (Table 4). Characters 1–5 involve lengths over a series of teeth and mainly estimated measurements are available. Characters 6–9 involve

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Fig. 9. Outlines of sabres or upper canines (C^1's) of Smilodontini and Homotheriini. Sabres are drawn to the same crown-root length for easy comparisons. Pillars to the left of the tips of the crowns indicate relative scales; associated figures give crown-root lengths in mm.

Smilodontini (upper row)

A *Megantereon megantereon* from Val d'Arno, Italy. Redrawn in reverse from Kurtén (1962, fig. 1).

B *Megantereon megantereon* from Puebla de Valverde, Spain. Redrawn in reverse from Kurtén and Crusafont (1977, fig. 15).

C *Machaerodus (Smilodon) gracilis* from Port Kennedy Caverns, Pennsylvania. Drawn from crushed facial specimen ANSP 44 in the Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.

D *Smilodon neogaeus* from Talara, Peru. Drawn from gracile specimen ROM:P 2120 in the Royal Ontario Museum, Toronto, Canada.

E *Smilodon neogaeus* from Talara, Peru. Drawn from robust specimen ROM:P 2228 in the Royal Ontario Museum, Toronto, Canada.

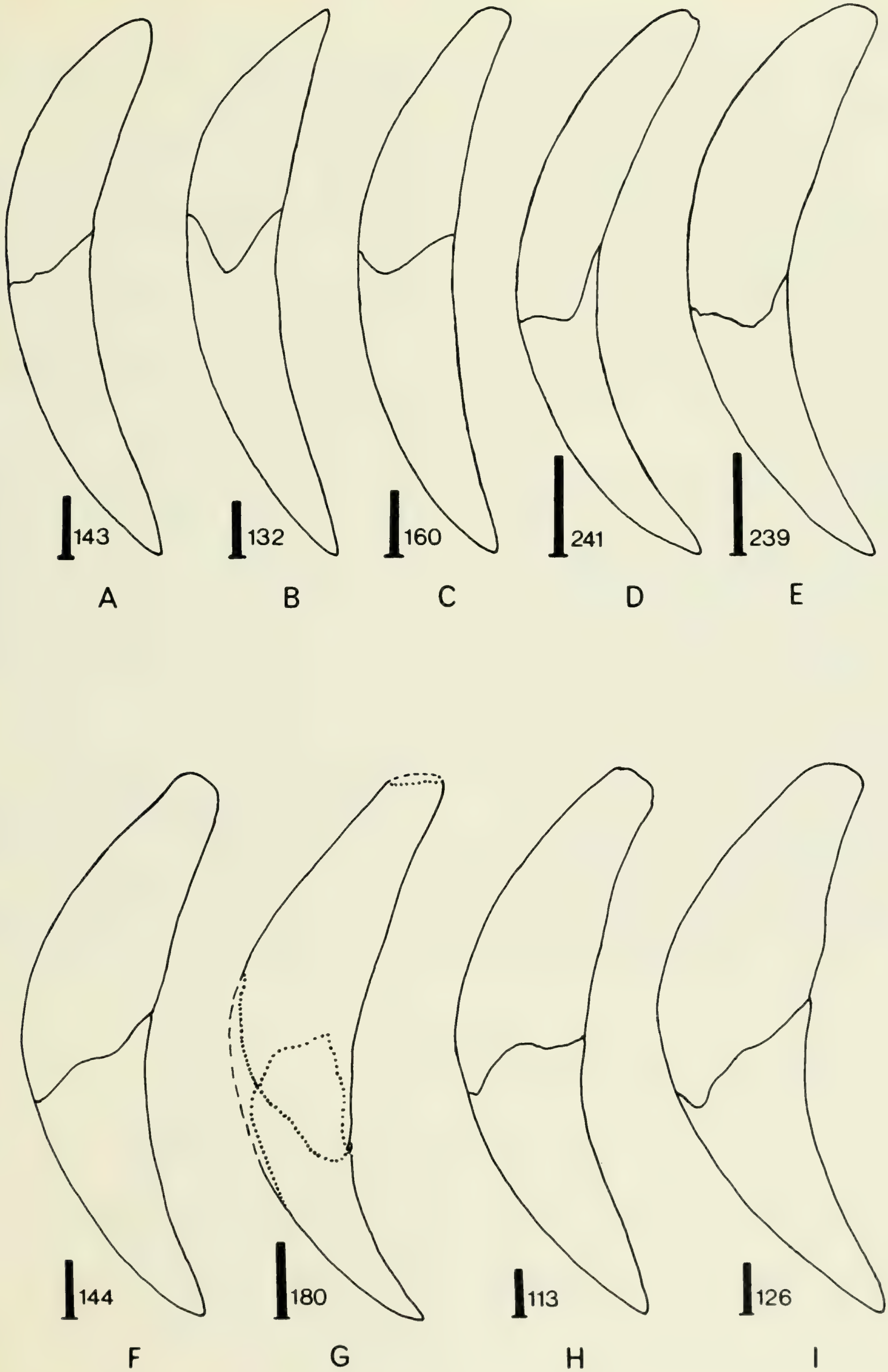
Homotheriini (lower row)

F *Machairodus crenatidens* from Val d'Arno, Italy. Redrawn in reverse from Kurtén (1962, fig. 1).

G *Homotherium crenatidens* (= *Ischyrosmilus johnstoni* partim) from Cita Canyon, Texas. Drawn from specimens WT 1026 (root) and WT 2429 (crown) in the Panhandle Plains Historical Museum, West Texas State College, Canyon, U.S.A.

H *Homotherium ultimum* from Choukoutien (Locality 13), China. Redrawn from Teilhard de Chardin (1939, fig. 3).

I *Homotherium serum* from the Friesenhahn Cave, Texas. Drawn from specimen TMM 933-1923, in the Texas Memorial Museum, University of Texas, Austin, U.S.A.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mesiodistal diameters of teeth in the symphyseal or diastematic regions. For Characters 6, 7, and 9 (mesiodistal diameters of I_2, C_1, and M_1) the overlap in measurements is at the lower end of the range and is probably not significant. For Character 8 (mesiodistal diameter of P_3) the larger overlapping measurement is estimated and the range of the P_3's for the Rancho La Brea and Talara *Smilodon* is founded on teeth which may or may not have been naturally present in life, as this tooth was undergoing reduction and is usually absent. Character 10 is the greater dimension of the symphysis and may be unreliable, as the symphyseal region has been distorted in both Port Kennedy mandibles. Characters 12 and 13 (depth of the dentary beneath P_3 and mesial to P_4) record small overlaps at the lower extremes of ranges that include estimated measurements and are also probably not significant.

The Port Kennedy sabretooth is smaller than *Smilodon* from Rancho La Brea and Talara in 38 of 44 dimensions (Table 5) but is similar to or overlaps the lower ends of the ranges for *Smilodon* in 6 dimensions. These dimensions are the trochlear diameter of the humerus, the proximal transverse diameters of metacarpal and metatarsal II, and three dimensions of the astragalus. As the sample available for the Port Kennedy sabretooth is inadequate for statistical treatment, it may be that the smaller sabretooth possessed elements that were either smaller or approached in size those of small individuals of the Pleistocene American *Smilodon*. The comparatively large astragalus and metapodials II suggest large extremities, and the dimensions of the calcar and astragalar facet on the calcaneum support this conclusion.

Tables 3–5 compare dimensions of the Port Kennedy sabretooth materials with similar data for *Smilodon* derived from the Rancho La Brea, California, and Talara, Peru, samples. In total, overlap of ranges occurs in only 30 of 134 dimensions available, and most occurs marginally at the lower limits of the size ranges for *Smilodon*. The Port Kennedy sabretooth is therefore considered to be dissimilar from the Pleistocene *Smilodon*, as was also concluded by Merriam and Stock (1932), in that it is generally smaller and more gracile, and differs in qualitative characters of the dentitions, skull, and mandible.

Table 6 gives measurements of Bass Point Waterway I and El Jobean Pit sabretooth materials. Comparisons of these with those of *Machaerodus gracilis* (including *M. mercerii*) from Port Kennedy show agreement in most dimensions for all elements except the sabre, C^1. Measurements of this tooth indicate that the Bass Point Waterway individual was considerably smaller than those from Port Kennedy and may reflect individual, geographic, or sexual differences. In all other dimensions the Bass Point Waterway and El Jobean Pit specimens are not significantly divergent in dimensions from the Port Kennedy Cavern *M. gracilis*, and I consider them to represent the same species.

The Haile XVA and Bass Point Waterway I remains are similar in details and size (Table 6). ROM:B 4238 has a well-developed astragalar foramen, about 4 × 2 mm in transverse and anteroposterior diameters, respectively, and a flattened outline to the navicular facet in broad aspect, as described for *Smilodon californicus* by Merriam and Stock (1932:142) and by Robertson (1976) for the Haile XVA specimen UF 17498. However, the medial calcanear and lateral navicular facets are not broadly confluent on the distal face of the astragalus, but only connected by an unfaceted ridge about 4 mm long.

SPECIFIC DISTINCTIONS BETWEEN *MACHAERODUS GRACILIS* AND *M. MERCERII*

Cope (1899) considered the Port Kennedy sabretooth to represent two species, although only one was described in 1880 and mentioned by him in 1895, and the second described in 1899. I found no significant divergences in conformation or size between *Machaerodus gracilis* and *M. mercerii*. Qualitatively the specimens resemble one another in all respects and quantitatively their dimensions

Fig. 10. Left lateral aspects of dentaries of Smilodontini and Homotheriini.
Specimens are drawn to similar incisive-condylar lengths. Bars beneath ventral margins represent 50 mm.

Smilodontini (left column)

A *Ischyrosmilus johnstoni* from Cita Canyon, Texas, U.S.A. Redrawn from Mawby (1965, fig. 2).

B *Ischyrosmilus ischyrus* from Asphalto, California, U.S.A. Drawn and restored from cast of UCMP 8140, Museum of Palaeontology, University of California, Berkeley, U.S.A.

C *Machaerodus (Smilodon) gracilis* from Port Kennedy Caverns, Pennsylvania. Drawn from dentary specimen ANSP 44, Academy of Natural Sciences, Philadelphia, Pennsylvania, U.S.A.

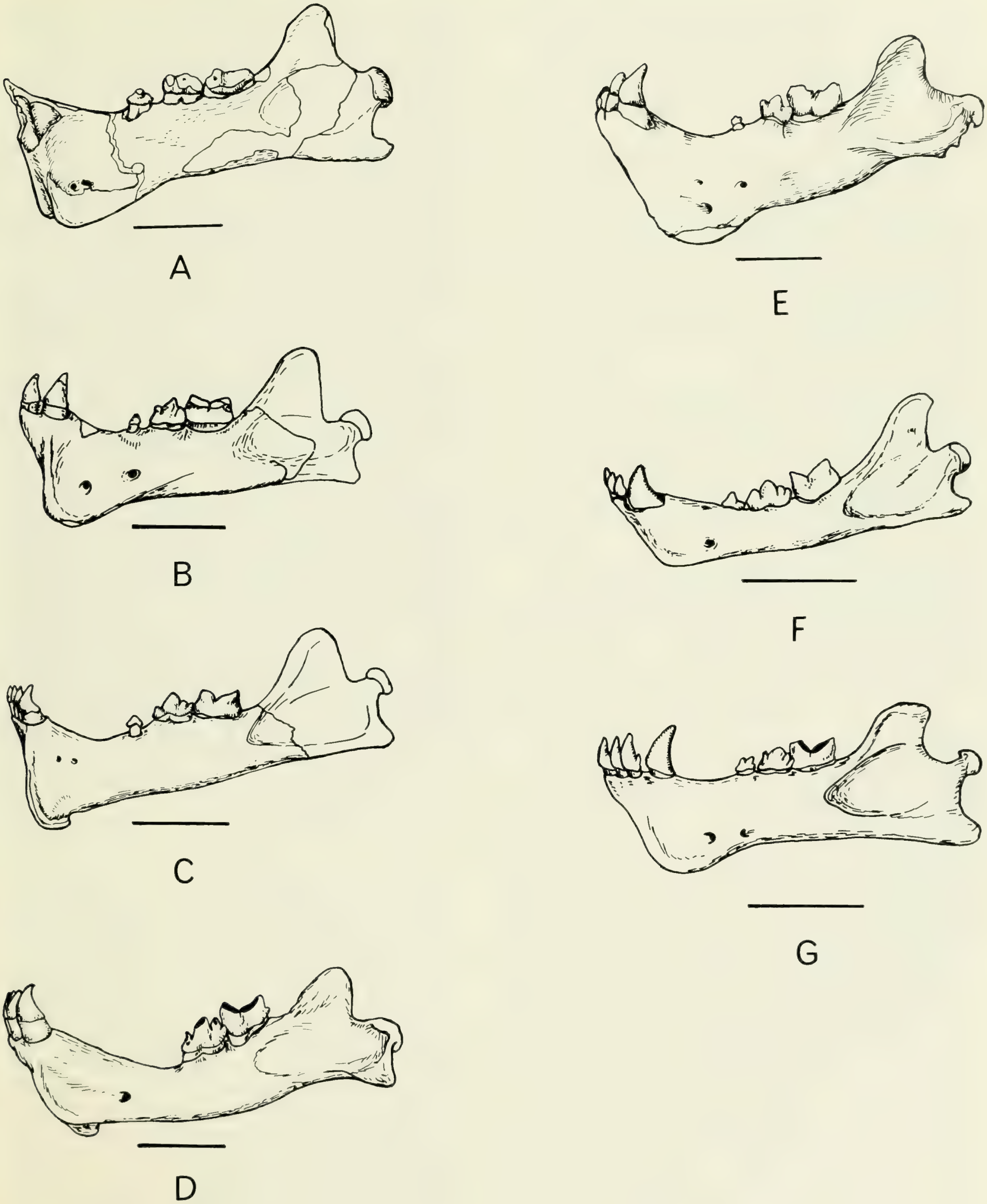
D *Smilodon neogaeus* from Talara, Peru. Drawn from robust specimen ROM:P2228, Royal Ontario Museum, Toronto, Canada.

Homotheriini (right column)

E *Homotherium nestianum* (= *Machairodus nestianus*) from Perrier, France. Redrawn from de Bonis (1976, fig. 5).

F *Homotherium palanderi* (= *Machairodus palanderi*) from locality 113, Pao-Te-Hsien, Shansi, China. Redrawn in reverse from Zdansky (1924, Tafel XXVI, fig. 2).

G *Homotherium serum* (= *Dinobastis serus*) from Friesenhahn Cave, Texas, U.S.A. Redrawn from Churcher (1966, fig. 1B).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vary less than do similar dimensions of *Smilodon* (Tables 3–5). Therefore these three individuals are considered to represent the species *Machaerodus gracilis* Cope, 1880.

Other specimens from Florida (Bass Point Waterway I, Sante Fe River Locality I, Inglis Locality IA, and Haile Locality XVA) resemble the Port Kennedy species wherever comparisons are possible. These specimens, except for the hitherto unpublished Bass Point Waterway and El Jobean Pit materials, from time to time have been referred to as *Smilodon gracilis* (Slaughter, 1963; Kurtén, 1965; Webb, 1974; Robertson, 1976; Kurtén and Anderson, 1980). The specific identity and distinctiveness is correct, but the generic assignation is questionable on the evidence discussed previously. It is thus necessary to reassess the generic status of the taxon originally named *Machaerodus gracilis* by Cope (1880).

AFFINITY OF *MACHAERODUS GRACILIS* WITH *ISCHYROSMILUS* MERRIAM, 1918

Resemblances between the Port Kennedy Species and Species Described within the Genera *Machaerodus* and *Ischyrosmilus*

Comparisons were made among the *M. gracilis* "type" materials from Port Kennedy, the Florida specimens, and other described North American sabretooth cats reported from the Pleistocene or late Pliocene.

Machaerodus ischyrus

Merriam (1905:173) considered the Port Kennedy sabretooth to resemble *Machaerodus* when compared with his new species *Machaerodus(?) ischyrus* from the late Pliocene of Asphalto, Kern County, California. He said: "Of the North American species *Machaerodus gracilis* Cope, from the Port Kennedy Fissure, resembles the California species in the form of P_3, while the heel of M_1 has almost disappeared. *M. ischyrus* differs from this species particularly in the shortness of the diastema and probably of the whole jaw, in the absence of a posterior basal cusp on P_4, and in the complete reduction of the heel of M_1. Judging from Cope's figure* (E. D. Cope, Jour. Philad. Acad. Nat. Sci., 2nd ser., vol. 11, pl. 20, fig. 1—footnote) of the type of *M. gracilis* the mandibular flange is not as prominent and the jaw as a whole somewhat weaker than in *M. ischyrus*." The measurements in Table 4 substantiate this estimation.

Merriam (1905) also compared *M. ischyrus* with *Smilodon fatalis, Dinobastis serus* (= *Homotherium serum*), *Felis imperialis,* and *M. catecopsis* but concluded that all four are distinct from *M. ischyrus*. He noted (1905:173) that *H. serum* did not "differ from *M. ischyrus* greatly in size and had large external incisors with a moderately elongated superior canine. The superior sectorial has a large protostyle, but the basal cusp anterior to this is rudimentary. This means that, as in *Hoplophoneus,* the posterior part of P_4 opposing it was probably relatively shorter than in *Smilodon*. The characters mentioned all suggest correlation with *M. ischyrus,* although there would at present be no justification for considering them identical." His conclusion is reasonable as *M. ischyrus* (known only from the anterior part of a dentary and later described as *Ischyrosmilus ischyrus*) was deduced to possess large sabre-like upper canines in contrast to the known prominent but relatively lower crowned, deltoid, and thinner canines of *H. serum*. Merriam also compared *M. ischyrus* with *M. palaeindicus* from the Upper Siwalik beds of India, which he considered resembled *M. ischyrus* greatly.

Merriam's type of *M. ischyrus* was referred to by Bovard (1907:163) as "characterized by the great reduction of P_3, the presence of a single posterior cusp on P_4, the absence of both metaconid and heel from M_1, the shortness of the diastema, the possession of a prominent flange below the symphyseal region and the abbreviation of the jaw." He concluded that "the presence of P_3 and the absence of metaconid and heel from M_1, the shortness of the jaw and the heavy flange indicate that *S. californicus* and *M. ischyrus* belong to widely separated species if not genera."

Brown (1908:191) wrote that *M. ischyrus* probably belonged to the genus *Dinobastis* "as indicated by the nearly equal size of paraconid and metaconid in m_1, and the erect position of p_4 without posterior basal heel. This correlation was suggested by Dr. Merriam." This suggestion was unfortunate as Merriam (1918) proposed the new genus *Ischyrosmilus,* for which he made *M. ischyrus* the type species.

Ischyrosmilus

The description of *Ischyrosmilus* is confusing. Merriam (1915:262) mentioned "*Ischyrosmilus* (Sabre-tooth cat)" from the Ricardo Pliocene but gave no description or discussion of the new generic name. In 1917 (p. 425) he noted that *Ischyrosmilus ischyrus* had been obtained from the Upper Pliocene (Tulare) of California, *Ischyrosmilus osborni* n. gen. n. sp. (= *Barbourofelis osborni, vide infra*) from the Lower Pliocene (= late Miocene) Ricardo of the Mohave Desert (p. 430), and "*Ischyrosmilus* n. sp." from the Upper Pliocene Snake Creek of Idaho, which he presumed represented "the Tulare stage in California" (p. 432). However, Merriam described neither the new genus nor the new species in this publication.

Ischyrosmilus idahoensis

Merriam (1918) gave the first description of the genus when he described *I? idahoensis,* and Simpson (1945) dated the genus from this description. However, *I? idahoensis* is not the type species, as Merriam (1918:524) described "*Ischyrosmilus,* new genus", founded upon "*Machaerodus? ischyrus*", in a footnote appended to the description of the new species "*Ischyrosmilus? idahoensis*". Merriam's (1918) remarks effectively parallelled those he gave later, in 1919, and constitute the first description of the genus. Merriam (1918) referred to the later publication as "in press". He (1918:524) described the new species *I? idahoensis* as differing from "the typical *S. californicus* in dentition by the presence of a small $P_{\overline{3}}$. . . . The Idaho mandible differs from that of *S. californicus* very decidedly in the size and proportions of the flange below the diastema. In *S. californicus* the flange is comparatively short, ending posteriorly rather abruptly some distance in front of $P_{\overline{3}}$. In no. 22343 the posterior end of the flange fades out below the anterior end of $P_{\overline{4}}$. A flange of this type seen in the Idaho specimen is found also in *Ischyrosmilus ischyrus* of the Tulare Pliocene of California, in *I. osborni* of the Ricardo Pliocene, and in *Machaerodus palaeindicus* of the upper Siwalik beds of India." Merriam added that the Idaho mandible is as large as that of *Smilodon californicus,* possesses P_3 and three mental foramina, and is tentatively dated as earlier than Rancho La Brea.

Osborn (1918:31) dated *I? idahoensis* as early Pleistocene or late Pliocene and referred to a sabretooth "resembling *?Machaerodus ischyrus*", presumably referring to the taxon rather than to an isolated tooth as no such specimen can be located.

Ischyrosmilus osborni (= *Barbourofelis osborni*)

Merriam (1919:543) reiterated the generic characteristics of *Ischyrosmilus* at length. This description is effectively the same as that in his 1918 footnote but with minor differences. The 1919 description, with textual divergences from the 1918 version in square brackets, reads: "Mandible massive; flange clearly marked, relatively wide anteroposteriorly, slightly deeper [wider] than in *Smilodon,* not as strongly developed as in typical *Machaerodus;* length of ["length of" omitted] diastema much as in *Machaerodus,* but shorter than in *Smilodon.* P_3 very small, with one root. P_4 with single posterior cusp or with ["with" omitted] incipient division of this cusp. [End of 1918 description.] M_1 without metaconid and heel. This group known only from beds referred to the Pliocene." Merriam considered the genus to be less advanced than *Smilodon. I. osborni* is said to be smaller than *I. ischyrus,* flatter in the anterior face of the symphyseal region, with much thinner or transversely narrower cheek teeth, and in the division of the posterior lobe of P_4 into two cusps. Hay (1927) mentioned only *I. idahoensis* in his review of the fossil Mammalia from the western states and dated it as Upper Pliocene or Lower Pleistocene, presumably following Osborn (1918).

Merriam (1919:545) described *Ischyrosmilus osborni* from the Ricardo Beds (Pliocene) near Red Rock Canyon, California, represented by a partial left dentary (UCMP 19476, holotype) with P_4 and damaged M_1, roots of I_1–I_3 and P_3, and alveolus for C_1. Merriam distinguished the species from others of the genus by its smaller size, transversely thinner cheek teeth, division of the posterior lobe of P_4 (?metaconid) into two cusps, and a flatter anterior face to the symphysis. He also remarked on the dorsoventrally narrow masseteric fossa beneath M_1, and speculated that this might indicate a different conformation to the jaw joint. The genial flange on the specimen is broken anteriorly and ventrally, so that the symphyseal face appears flatter in lateral aspect. P_3 is single rooted, and shows no sign of a double origin. P_4 and M_1 are as in other *Ischyrosmilus,* except for the double-cusped metaconid on P_4, which is possibly formed from the talonid.

The characters described by Merriam (1919) are those selected by Gregory (1942), Kitts (1957), and Mawby (1965) to separate the Ricardo "*Ischyrosmilus*" *osborni* from other *Ischyrosmilus.* Schultz, Schultz, and Martin (1970) placed "*I.*" *osborni* in their new genus *Barbourofelis* but mentioned only three of the characters enumerated by the earlier authors.

Ischyrosmilus johnstoni

Johnston and Savage (1955:39) listed "*Ischyrosmilus* or *Homotherium*" from the Blancan (Plio-Pleistocene) of Cita Canyon, Texas. This tentative identification was based on a restored skull composed of separated facial and cranial sections (WT 1860) and a mandible (WT 1239) which derive from individuals the size of *Homotherium* or *Smilodon.* Other cranial, dental, and postcranial materials are associated with these two specimens and have been compared with materials of other large sabretooths. Also, a cast of the restored skull and mandible (ROM 30136 = WT 1860 + 1239) was available for study in the Royal Ontario Museum.

Mawby (1965) described the Cita Canyon machairodont materials originally reported by Johnston and Savage (1955). He described a new species, *Ischyrosmilus johnstoni,* based on the mandible (WT 1239, holotype) and referred to it other mandibular specimens (UCMP 66486 [= WT 1834], WT 1238, 2615), cranial specimens (WT 1860,

UCMP 66485), and isolated canine specimens (WT 1026 [= 1025], 1026, 1528, 1834, 2429). Some fragmentary postcranial specimens (humeri, WT 625, 1691, UCMP 66487, unnumbered; ulna, WT 628; femora, WT 626, 1066, UCMP 66488; tibia, UCMP 66489) are tentatively referred to *I. johnstoni*. Mawby (1965:583) compared *I. johnstoni* with *I. ischyrus* and *Smilodon californicus*, but "no close relationship between the two genera is implied. On the contrary, *Smilodon* and *Ischyrosmilus*, respectively, represent two quite distinct machairodont lineages, for which Kurtén (1963) has proposed the tribal names Smilodontini and Homotheriini." (Churcher [1966] incorrectly cited Kurtén as proposing two subfamilies, Smilodontinae and Homotheriinae.)

Mawby (1965:584) compared *I. johnstoni* with Eurasian *Homotherium* and concluded that "there are many similarities between *Homotherium crenatidens* [from the Villafranchian of Europe and Asia] and *Ischyrosmilus johnstoni*. Both were long-limbed, relatively slender animals, with deep massive mandibles. The dentitions are similar, with relatively short, flattened sabres, and high, narrow carnassials. There are numerous points of resemblance in the skull, including the form of the mastoid process, the shape of the bulla, the keel and depressions of the basioccipital and division of the sagittal crest. It is likely that direct comparison of *I. johnstoni* with specimens of *H. crenatidens* would show the two to be congeneric." This discussion will show that Mawby's (1965) conclusions are partly erroneous, as two sabretooth cats, one of which is a homothere and the other a smilodont, are represented in the material assigned to *I. johnstoni*.

In *Homotherium* (Fig. 11) the incisors are set in a rounded arcade and are equally spaced, the sabres are proportionately more laterally compressed and only mediumly hypsodont compared to other machairodonts, P^3 is small but always present, P^4 is a two-rooted vertical blade lacking all remnants of protocone or protoradix in the late Pleistocene or Holocene species, and M^1 is a more or less styliform tooth with a triangular crown. In the lower jaw, P_3 is two-cusped and more hypsodont, and P_4 and M_1 are hypsodont and show a vertical pattern of wear. All teeth in *Homotherium*, whether milk or permanent, are serrated, and all incisors possess mesial and distal cuspules that are also serrated (Churcher, 1966). Another character that appears to be distinctive in the facial region is a small elongate oval infraorbital foramen, which is divergent from the larger and broader infraorbital foramina typical of smilodonts.

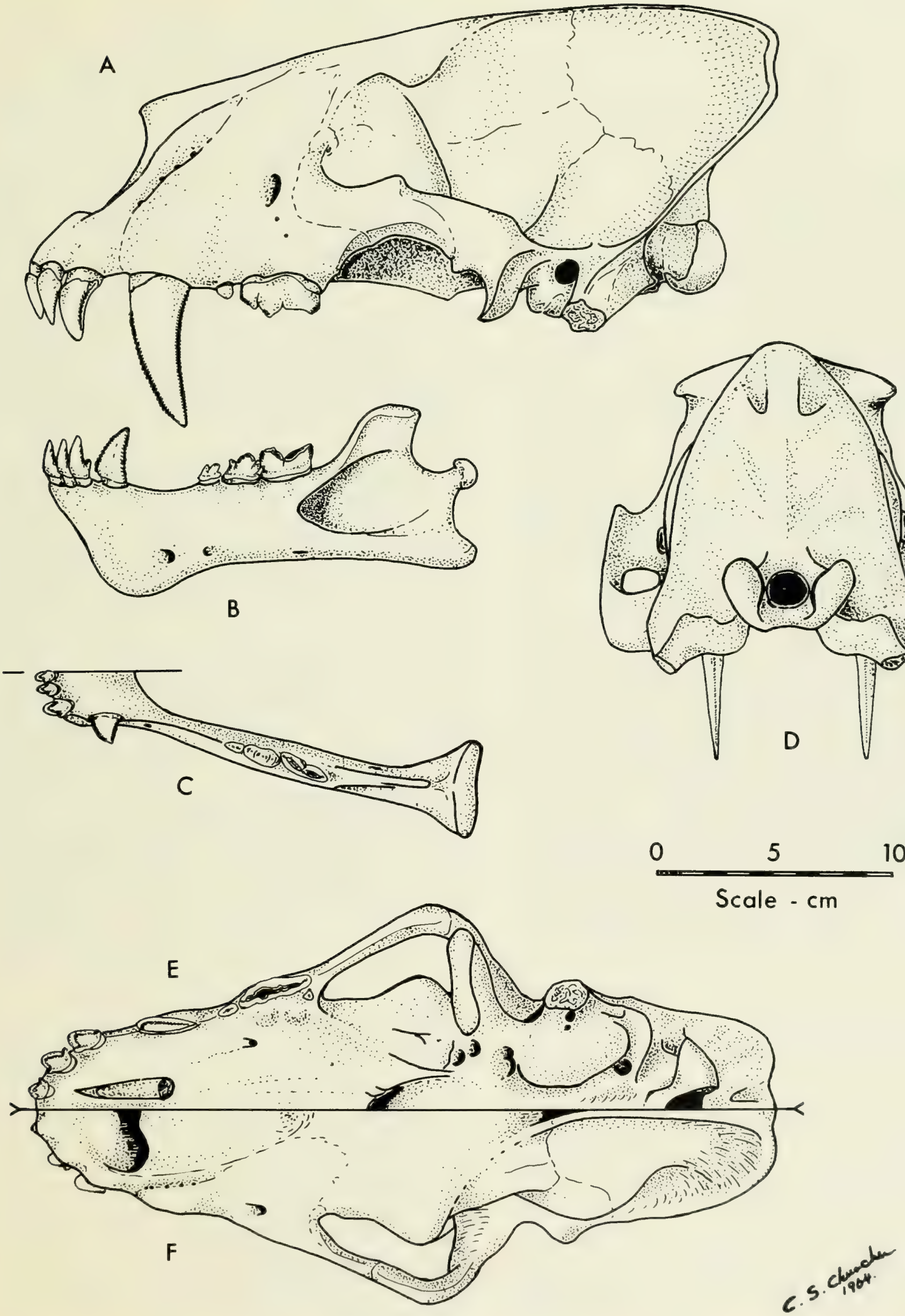
Fabrini (1890) established *Homotherium* on *Machairodus crenatidens* and *M. nestianus*. Cope's (1893) *Dinobastis serus* from North America morphologically resembles the Chinese *H. ultimum* (see Churcher, 1966) and, as has been reviewed above, *Ischyrosmilus* (based on *I. ischyrus*) is not congeneric with *Homotherium* or even closely allied to it. Mawby (1965:580, fig. 3) illustrated a specimen with P_4 and M_1 (WT 1238) with enlarged detail drawings of crenelations on the mesial margin of the protoconid of P_4, a mesial flange on M_1, with crenelations on its margin, and a slightly damaged protoconid. As the type mandible (WT 1239) possesses only well-worn teeth, Mawby (1965:577–578) referred the teeth on WT 1238 to *I. johnstoni* and ascribed their characteristics to his new species.

Churcher (1966:267) described P_4 and M_1 of the Friesenhahn Cave, Texas, *Homotherium serum* thus: "The fourth lower premolar is absolutely smaller than that in *Smilodon* and does not show an incipient mesial or distal style. In the unworn condition all three major cusps show fine serrations. The lower molar is set closely distal to or slightly overlapping P_4, and both P_4 and M_1 have distally tilted crowns. In absolutely unworn erupting M_1's, the whole mesial, distal, and occlusal edges of the crowns are serrated, especially the mesial and distal surfaces; M_1 is proportionately more buccolingually flattened. . ." than P_4.

The characteristics of P_4 and M_1 in *H. serum* are equally descriptive of teeth in WT 1238 from Cita Canyon, with the reservation that Mawby's illustration tilts the occlusal plane some 15° from the horizontal and thus provides a distad tilt to the teeth. I observed serrations on P_4 and M_1 teeth in *H. serum*, and Figure 4 (reproduced from Churcher, 1966:266) illustrates their extent. The referred specimen WT 1238, from which the lower cheek teeth of *I. johnstoni* were described, therefore derived from *Homotherium*. Consequently, some of the other referred

Fig. 11. *Homotherium serum* (Cope, 1893). Reconstruction of skull and mandible of the Friesenhahn Cave scimitar-tooth from Churcher (1966). Reconstruction based mainly on specimens in the Texas Memorial Museum, Austin, Texas (skulls TMM 933-3231 and 3582 and mandible TMM 933-1) with additional details from isolated teeth and elements from the Friesenhahn Cave and specimens from Kansas and Oklahoma. Scale in centimetres.

A Lateral aspect of skull.
B Lateral aspect of left dentary.
C Occlusal aspect of mandible.
D Nuchal aspect of skull.
E Ventral aspect of left side of skull.
F Dorsal aspect of left side of skull.


A
B
C
D
0 5 10
Scale - cm
E
F
C. S. Churcher 1964.

specimens or probably referred postcranial elements could also derive from an individual of *Homotherium*.

Mawby (1965:576) listed two fragments of upper canines (WT 1026, 2429) among the referred materials. In 1966 the late Dr. C. W. Hibbard and I examined these fragmentary specimens (and most of the other material assigned to *I. johnstoni*), then at the Museum of Paleontology, University of California, Berkeley, and we concluded that they probably derived from a homothere because of the mesiodistally wide alveolar region, the relatively short crown height or medium development of hypsodonty, the more acute angle between the axes of the crown and the root, and the configuration of the enamel margin and the serrated mesial ridge (Fig. 9G). Kurtén (1962:103, fig. 1) gave outline comparisons of sabres of *Megantereon* and *Homotherium crenatidens* from Val d'Arno (Fig. 9A,F). Mawby's (1965:586, fig. 5) illustration and cast of the skull (WT 1860) show a restored sabre that is more hypsodont and slender than are those in the Friesenhahn Cave *H. serum*, very worn P^4's that curve inwards as only in very old individuals, no P^3's or M^1's, but alveoli for both M^1's, and possible traces of resorbed alveoli for the P^3's (Fig. 12C). He described P^3 in UCMP 66485 as possessing two well-developed separate roots as determined by the alveoli. The P^4's are too worn to reveal any of the crown's details. Their roots are shorter than in *S. californicus* and there are separate roots that either supported a protocone or just buttressed the crown. The infraorbital foramen is oval and about half the size of that in *Smilodon*. The incisors appear to have been set in a more rounded arc than in *Smilodon*, since all three are visible in lateral aspect, as in *Homotherium*, but are too worn to reveal their crown morphology.

The characters on the facial fragments indicate that UCMP 66485 probably represents a homothere because of the presence of P^3, as does WT 1860 (facial region) because of the small infraorbital foramina, the strongly concave or deep palate and the incisors set in an arc. The distance from the sabre to the mesial margin of P^4 is short and could not support a fully developed three- or four-cusped P^3 (as in *M. gracilis* or *Smilodon*) but could accommodate a small single- or double-cusped tooth with fused or closely set roots as in *Homotherium* (Table 3).

Measurements available from the dentitions and skull of the Cita Canyon specimen's facial region (WT 1860, Table 3) show that all dimensions are absolutely greater than any from the type specimens of *M. gracilis* or *M. mercerii*, except for the crown height of the sabre, C^1, which is less. These measurements generally lie within the size ranges for *Smilodon* and *Homotherium serum* and indicate that the Cita Canyon facial specimen derived from an individual larger than the Port Kennedy Caverns sabretooth and as large as either *Smilodon* or *H. serum*. Among the other Cita Canyon material are canines that are similar in height and proportions to those of *H. serum* (Fig. 9G).

The entire C^1 (WT 1025; listed as 1026 by Mawby, 1965) is estimated by Mawby as 150 mm in overall length. C. W. Hibbard and I estimated the same dimensions for the combined WT 1026 and 2429 as 160 to 165 mm. Sabres in the Port Kennedy *M. gracilis* are about 160 mm long, although the total length had to be estimated as the roots are still implanted and the six sabres of the Friesenhahn Cave *H. serum* range between 118 and 126 mm in total length. Although the size of WT 1025 and the composite figure based on WT 1026 and 2429 more closely approach that for *M. gracilis*, their conformation indicates affiliation with homotheres and not with smilodonts. Mawby (1965:78) commented: "Near the root, the anterior edge of WT 1025 turns somewhat medially, less sharply than in *Dinobastis* but much as in *Smilodon*," which suggests that WT 1025 represents a smilodont and disagrees with C. W. Hibbard's and my observations based on WT 1026 and 2429.

Specimens WT 1528 and 1834, both fragmentary sabres, are not discussed by Mawby, although measurements of WT 1834 are given with those of WT 1025 (Mawby, 1965:578, table 2—as 1026). As WT 1025 is considered to derive from *Homotherium*, perhaps WT 1834 does also, for its measurements fall within the range of variation of C^1's for that genus.

The cranial portion of WT 1860 is not directly comparable with the type of *M. gracilis*, which lacks that region, but is comparable with those of *H. serum* and *S. californicus* (Fig. 12). Mawby (1965:581, fig. 4) illustrated and described the basicranial region of *I. johnstoni* but compared it only with *S. californicus*. A major diagnostic difference between a smilodont and a homothere is the degree of closure of the ventral re-entrant into which the external auditory meatus opens; that is, whether the mastoid process lies close to the posterior surface of the glenoid process or not. In *S. californicus* the separation is from 1 to 2 mm, and in *H. serum*, it is about 20 mm. Mawby's figure 4 shows a wide separation that is about 15 mm on the cast, and he (1965:580) stated that the mastoid does not approach the glenoid process.

Other characteristics of homotheres are also present in the basicranial region. The foramen ovale is separated from the eustachian canal by a ridge of bone in *Smilodon* and by a flat area in *Homotherium* and in WT 1860. The stylomastoid foramen is separated from the tympanohyal pit in *Smilodon* by an area of the wall of the bulla, but in *Homotherium* they are apposed because of the posterior inclination of the mastoid process, as in WT 1860. The basioccipital-basisphenoid has a central ridge that ends anteriorly in two round pits at the level of the mastoid and slightly posterior to the midpoint of the bullae in WT 1860, as in *Homotherium* but not in *Smilodon*, where the ridge continues to the level of the eustachian canal, bifurcating

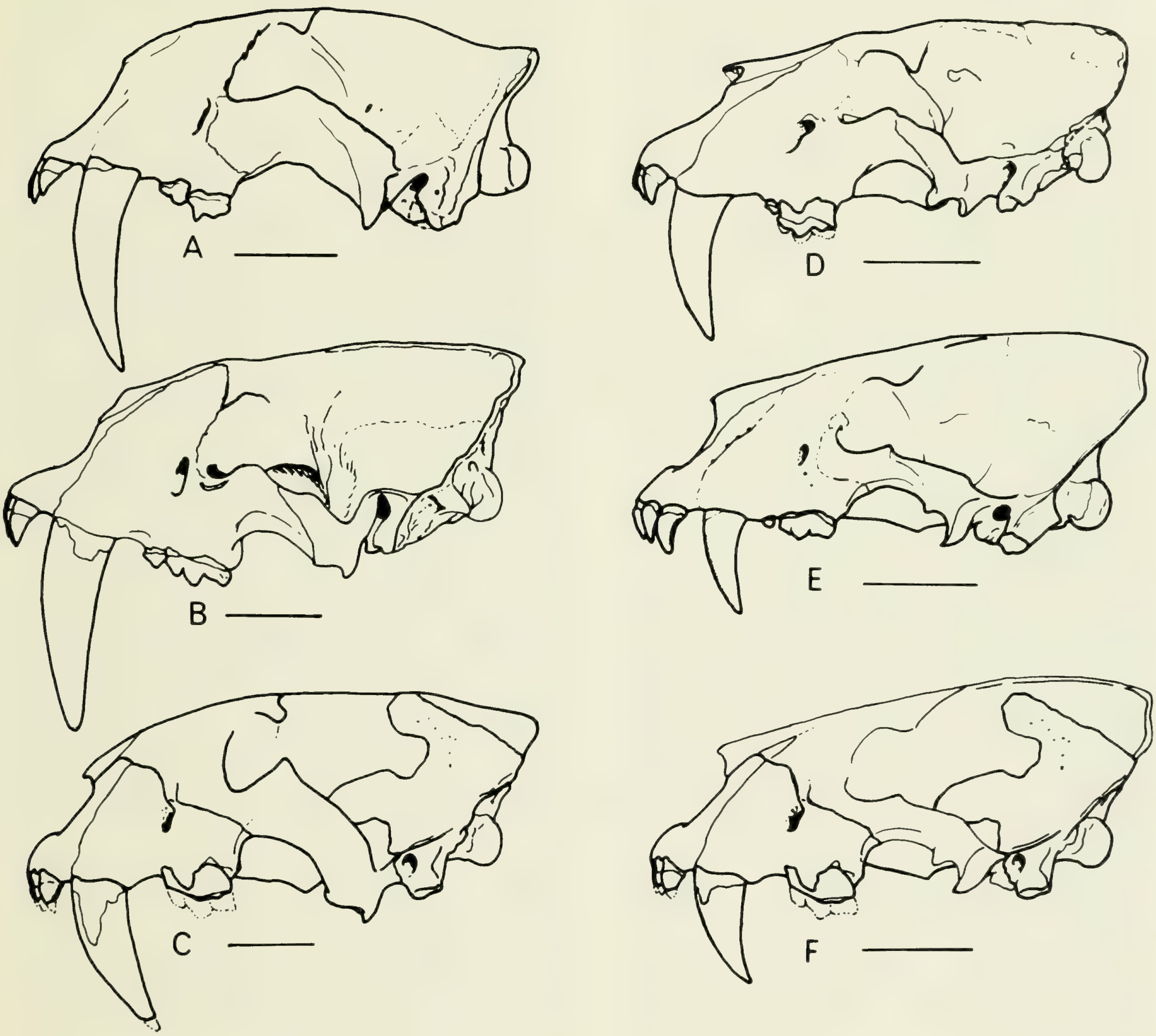


Fig. 12. Left lateral aspects of skulls of Smilodontini and Homotheriini, with restorations of the fragmentary skull of *Ischyrosmilus johnstoni* Mawby, 1965. Specimens are drawn to similar basicranial lengths. Bars beneath the ventral margins represent 50 mm.

Smilodontini (left column)

A *Megantereon megantereon* from Senèze, France. Redrawn from Piveteau (1961, fig. 172).

B *Smilodon floridanus* (= *S. californicus*) from Rancho La Brea, California, U.S.A. Redrawn in reverse with sabres restored to in vivo position from Merriam and Stock (1932, pl. 1, fig. 1).

C *Ischyrosmilus johnstoni* from Cita Canyon, Texas, U.S.A. Redrawn from Mawby (1965, fig. 5).

Homotheriini (right column)

D *Homotherium nestianum* (= *Machairodus nestianus*) from Perrier, France. Redrawn from de Bonis (1976, fig. 8a).

E *Homotherium serum* (= *Dinobastis serus*) from Friesenhahn Cave, Texas, U.S.A.. Redrawn from Churcher (1966, fig. 1A).

F *Homotherium* sp. (= *Ischyrosmilus johnstoni* partim) from Cita Canyon, Texas, U.S.A. Redrawn with facial and basicranial fragments WT 1860 reoriented within the outline of a *Homotherium* skull and with a homothere sabre to illustrate a more likely conformation.

and ending near the roots of the alae. Mawby (1965) also reported that the sagittal crest bifurcated posterior to the parietals, as in *Homotherium* but not in *Smilodon*.

The cranial and facial parts of WT 1860 are thus assigned to *Homotherium* as both differ in all observed characters from those found in smilodonts, including *Ischyrosmilus*. The single fragment of the cranium of *M. gracilis* recovered from Bass Point Waterway I (ROM:B 4733, Figs. 1B, 2C) has a ventrally closed external auditory opening, with the mastoid process apposed to within 5 mm of the posterior glenoid surface. This small fragment indicates that the condition in *Ischyrosmilus* was probably typical of smilodonts but not as derived as in *Smilodon*.

The type mandible of *I. johnstoni* (WT 1239), of which the left dentary is illustrated by Mawby (1965:579, fig. 2), has been broken through the diastema at the level of the posterior mental foramen; the condylar and angular area is separated from the coronoid and body; the mental flange, parts of the ramus beneath P_4 and M_1, and a small area posterior to M_1 are missing; and the buccal walls of the incisive and canine alveoli are absent.

Comparison of the type mandible of *I. johnstoni* WT 1239 with the type of *M. gracilis* ANSP 44 is informative (Figs. 10A and C). The dentaries of *M. gracilis* are well preserved but compressed anteriorly and may be used as a standard for comparison. The incisors and lower canine were set with their crowns in a slightly bowed transverse row, as is suggested by both the type and the Cita Canyon dentary WT 1239. The mental foramina are double, although not as well separated, and without a subdivision of the anterior foramen. This could be explained in WT 1239 by the absence of the posterior foramen and by the separation of the twinned openings of the anterior foramen. P_3 is small, with two fused roots, and occurs separated mesially from P_4 in all specimens examined. P_4 and M_1, where preserved, are similar in morphology and in distal inclination to those in the type of *M. gracilis*. The ventral margin of the ramus, the slopes of the anterior margins of the coronoids, and the conformation of the masseteric fossa are all similar to those of the type of *M. gracilis* but only fragments of the latter two are available. In WT 1239 the margin of the mental flange is absent. This area is preserved in the type of *M. gracilis* and shows a posterior step below the mental foramen, which may be unusual for the taxon.

The type mandible of *I. johnstoni* (WT 1239), that of *M. gracilis* (ANSP 44), and casts of a right dentary from Inglis IA (UF 20065) ascribed to *Smilodon gracilis* by Webb (1974) are similar. Both WT 1239 and UF 20065 are broken in the incisive and canine alveolar regions in an almost identical manner and have lost comparable areas of the condylar, coronoidal, and angular regions. Morphologically these specimens are conformationally identical. However, the Inglis IA specimen is linearly about 70 per cent the size of the Cita Canyon specimen and presumably is from an animal as small as those from Haile XVA (Robertson, 1976) or Bass Point Waterway I and slightly smaller than the type dentaries of *M. gracilis* from Port Kennedy Caverns.

Mawby's (1965:586, fig. 5) reconstruction is thus a composite. The jaw is the type of *I. johnstoni* and is correctly considered similar to other *Ischyrosmilus*, but it also resembles *M. gracilis* and other specimens that are usually referred to in the literature as *Smilodon* or *Smilodontopsis gracilis*. The skull derives from a homothere, somewhat more primitive than *H. serum* from Texas. No contacts are present between the facial and cranial portions of WT 1860, and error has been introduced in the reconstruction because the cranial portion has been placed lower with respect to the palatal plane than it should be and also because the glenoid-mastoid-occipital-condylar alignment has been tilted at about 30° to the occlusal plane rather than about 20° as in *Homotherium* (Fig. 12C). In *Smilodon* the inclination is about 40°. This placement accommodated the *Ischyrosmilus* jaw, allowing it to have the space for opening, but in *Smilodon* the glenoid is placed well above the palatal and occlusal planes, and in *Homotherium* it lies only slightly above these planes. This ventral displacement further distorts the cranial outline of the skull, which becomes nearly parallel to the basicranial and palatine planes instead of rising distally to a high lambda, as in *Smilodon* and *Homotherium* (Fig. 12B,E). When relative positions of the fragments are altered, the skull outline and basicranial and palatal relationships conform to the normal homothere configuration (Fig. 12F).

The specimens referred by Mawby (1965) to his new species *Ischyrosmilus johnstoni* thus derive from two different sabretooth species, one a homothere and the other a smilodont. The type mandible represents the smilodont *I. johnstoni*, and the skull is that of a species of *Homotherium* which is more primitive than *H. serum*. *I. johnstoni* is represented by the type specimen: a mandible with right and left P_4's and M_1's, left P_3, roots of left C_1 and right P_3, all heavily worn (WT 1239), a partial right dentary (UCMP 66486, ex WT 1834), an edentulous, possibly juvenile, left dentary (WT 2615), a left maxilla with P^4 (UCMP 66485), and an isolated sabre (WT 1025 = WT 1026 in Mawby's list of materials). The genus *Homotherium* is represented by a fragment of a right mandible with nearly unworn P_4 and M_1 (WT 1238), a left maxilla with I^1–I^3, P^4, stump of sabre and two separated cranial fragments (WT 1860, restored as a skull), and two fragments of sabres (WT 2429 crown, WT 1026 root). Another fragmentary sabre (WT 1528) is unassigned.

Mawby (1965:581–582) gave a number of measurements for postcranial elements that he considered probably

derived from *I. johnstoni* and commented that "they indicate that *Ischyrosmilus* was a long-legged animal, probably with a slender build like that of *Homotherium* (Schaub, 1925) rather than the squat proportions of *Smilodon* or the sloping stance of *Dinobastis* (Meade, 1961)." As *Dinobastis* and *Homotherium* are congeneric (Churcher, 1966), this statement should be modified to emphasize the long-leggedness of the homotheres contrasted to the heavy build of the smilodonts.

When measurements of the postcranial elements of the sabretooths from Cita Canyon are compared with those given by Meade (1961) for *Homotherium serum* (Table 7), the humeri (WT 625, 1691, UCMP 66487) are found to be smaller than for *Smilodon* and slightly smaller than for *H. serum*. Mawby (1965) noted that these humeri generally are similar to the humerus of *Machaerodus catacopsis* from the Hemphillian of Texas. The humeri may therefore be derived from *Ischyrosmilus*, as they appear to be of about the appropriate size and morphology for a smilodont smaller than *Smilodon* and about the size of *M. gracilis*.

The ulna (WT 628) appears to be smaller than the ulnae of both *Smilodon* and *Homotherium* from the few data available, and may also be derived from *Ischyrosmilus*. The femur (WT 1066) is as long as that of *Smilodon* and some 12 per cent longer than the femora of *Homotherium serum* from Friesenhahn Cave, Texas. The other femoral measurements approximate those of *H. serum* and *S. californicus*, except those of the caput and condyles, which are less than in *S. californicus*. In these latter dimensions WT 1066 and UCMP 66488 resemble *Homotherium*.

The tibia (UCMP 66489) resembles the tibiae of both *Smilodon* and *Homotherium* in its measurements. However, as Mawby stated, it is long and slender. Both the femora and tibia are long, longer than might be expected to correspond to the humeri and ulna, and slenderly built. Mawby (1965) noted that the morphology of the suture joining the lesser trochanter on the femur to the greater trochanter resembled that in *Homotherium*. Thus the femora and tibia probably derive from a homothere and may be associated with the skull and other elements identified above as *Homotherium*.

The postcranial elements thus represent both a smilodont and a homothere, with humeri (WT 625, probably WT 1691, UCMP 66487) and the ulna (WT 628) from *Ischyrosmilus johnstoni* and the femora (WT 1066, UCMP 66488) and tibia (UCMP 66489) from *Homotherium*.

Ischyrosmilus crusafonti

Schultz and Martin (1970) described *Ischyrosmilus crusafonti* from a partial left dentary (UNSM 25493) with well-worn C_1, P_4, and M_1, crownless I_3, and alveolus for P_3, and referred a partial upper sabre (C^1 UNSM 25503) to that species. Both specimens derived from the early Pleistocene Lisco Member of the Broadwater Formation on the Dan Bowman Ranch, near Broadwater, Merrill County, Nebraska.

The species is diagnosed as the "smallest known species of [the] genus; P_3 single-rooted, but proportionately large" by Schultz and Martin (1970:34), who commented that the dentary is "considerably smaller and more lightly built than the holotype (ramus) of *Ischyrosmilus ischyrus* Merriam, but it resembles the latter in most other respects." Measurements of the described dentaries of *Ischyrosmilus* (Table 4) show *I. crusafonti* to have measurements that differ from those of *I. ischyrus*, whether taken by Merriam (1905, 1918), Schultz and Martin (1970), or Kurtén (1982, pers. comm.), by being 2 to 4 mm smaller, and thus cannot be said to be "considerably smaller" in such a large animal. When the observed ranges of variation of similar dimensions for the better-known sabretooth *Smilodon* are used as a standard, all measurements for any one dimension on available specimens of any species of *Ischyrosmilus* fall within a smaller range than exists in *Smilodon*.

The dentary USNM 25493 possesses a damaged genial flange, a twinned foramen on the lateral face of the flange, and a second mental foramen beneath P_3, as in *I. johnstoni*. Such a morphology is present also in the Port Kennedy *M. gracilis* jaws and the Inglis IA (UF 20065) dentary. Schultz and Martin (1970:34) stated "The incisors of *I. crusafonti* are caniniform, each consisting of a single cusp which is recurved posteriorly. The incisors and canines are serrated. . . . The I_1 is small and compressed while I_2 and I_3 become progressively larger. The [lower] canine is relatively large for a machairodont cat." Schultz and Martin (1970:35, fig. 1B) illustrated buccal and occlusal aspects of the dentary and showed no serrations or curvature on the lower incisors or canines but did show that the crown of I_3 is missing, that of C_1 worn to a stub, and those of I_1 and I_2 worn or faceted. The P_3 was small, separated from P_4 by about 8 mm, and possessed a fused double root, of which the mesial portion was half the diameter of the distal. The size and position agree with those of the P_3's observed in *M. gracilis* and other *Ischyrosmilus*, although the proportions of the fused roots vary.

Schultz and Martin (1970:34) stated "The P_3 appears to have been proportionately larger than that in *I. ischyrus*." The measurements given in Table 4 for the alveolus are not comparable to those of crowns of P_3's as P_3 is usually tilted distally, and thus the alveolar margin traces an oblique line across the face of the root, and because cingula on the crown make measurements of crowns greater than those of roots that support them. They further stated "The P_4 of *I. crusafonti* is slightly recurved posteriorly and has two roots. It consists of a paraconid, a

larger protoconid and a metaconid about equal in size to the paraconid. An accessory cusp (talonid) also may have been present posterior to the metaconid, but the tooth is too worn to be certain of this."

Schultz and Martin (1970:35, fig. 1B) illustrated the P_4 in both buccal and occlusal aspects. The paraconid is well preserved but heavier than in other *Ischyrosmilus* or *M. gracilis,* the protoconid is higher and similar in section to the metaconid, but both the latter are too worn to be certain of details. In *Ischyrosmilus* the protoconid is large, almost three times the mesiodistal length and twice the height of either the paraconid or metaconid, and the talonid is a distinct distal or distolingual shelf. These characters are not discernible in Schultz and Martin's diagrams. Both P_4 and M_1 are well worn distal to the protoconid of P_4, and some characters described by Schultz and Martin may no longer be present on the specimen.

Schultz and Martin (1970:34,35, fig. 1A) also reported *Ischyrosmilus* sp. from the early Pleistocene Lisco Member of the Broadwater Formation but from Garden County, Nebraska. This identification is based on UNSM 1105, which comprises left and right damaged premaxillae and left and right I^2, I^3, and C^1. The sabres are curved as in *Smilodon* and appear to have slipped from the sockets 10 or 15 mm. Schultz and Martin (1970:34) note that this specimen is "larger than *Ischyrosmilus crusafonti* from the Broadwater Local Fauna, and is near the size of *I. johnstoni* Mawby. The canines are proportionately shorter than in *Smilodon* although they are almost as broad. They are also more coarsely serrated." Schultz and Martin (1970, fig. 1A,C) figured the premaxillae and sabres (UNSM 1105) of *Ischyrosmilus* sp. and a partial left upper canine (UNSM 25503) assigned to *I. crusafonti* to the same scale (3/5). These diagrams show both sabres to have equivalent mesiodistal diameters at the bases of the crowns (18 mm on figures = ± 30 mm actual) and to be comparable in outlines. Dr. Björn Kurtén measured the gross dimensions of the teeth in both specimens, and these measurements agree with those for other *Ischyrosmilus* specimens available and for *M. gracilis* (Tables 3, 4). No basis of comparison exists for stating that UNSM 1105 is from a larger individual than the type of *I. crusafonti,* as all the Nebraska specimens agree in dimensions with those recorded for *M. gracilis.*

The sabres of UNSM 1105 (Schultz and Martin, 1970, fig. 1A) are similar to those of *Smilodon* in curvature and robustness, rather than to those of *Homotherium* (Fig. 9H,I). "The incisors in UNSM 1105 are arranged in a broad curve anterior to the canines, and are large and widely spaced. They show distinct wear facets in the regions where they interlocked with the lower incisors, as in *Smilodon*" (Schultz and Martin, 1970:34). In fact the incisors lie in a shallow curve, with I^1's and I^2's located on a transverse axis and I^3's slightly posterior to it. The wear facets show truncations of the crown from edge-to-edge bites, as in *Smilodon,* and show the effects of both crown-to-crown and interlocking occlusions. The size of I^1's is unknown, as they are absent and the alveoli damaged, but they were subequal to or smaller than I^2's from the space available.

The specimens described as *Ischyrosmilus crusafonti* (UNSM 25493, partial dentary, and UNSM 25503, partial sabre) and *Ischyrosmilus* sp. (UNSM 1105, partial premaxillae with sabres), all from the Lisco Member of the Broadwater Formation of early Pleistocene age from Nebraska, do not differ significantly either qualitatively or quantitatively from the range of specimens previously described within *Ischyrosmilus,* and the dentary closely resembles the type of *I. ischyrus.*

THE CITA CANYON HOMOTHERE

This *Homotherium* may not be considered as *H. serum* with confidence because of the Blancan age of the Cita Canyon fauna and the late Pleistocene age of the Friesenhahn Cave remains (a dischroneity of some 2×10^6 years), and because of the longer limb bones and morphological differences in the basicranial and dental characteristics, although the cranial and dental dimensions of the Cita Canyon specimens generally fall within extremes of size observed in the Friesenhahn Cave *H. serum.*

Cranial material of the Cita Canyon *Homotherium* is distinguishable from that of the Friesenhahn Cave *H. serum* on the following characteristics:

1. The incisors are not set in as rounded an arcade and are not as separated from each other.
2. The sabre (C^1) is more hypsodont and may be considered intermediate between *H. serum* (or *H. ultimum* of China) and a less specialized serrated condition.
3. P^3 is small and two-rooted (not single-rooted as in *H. serum*).
4. The upper carnassial (P^4) has a protoradix.
5. Serrations on P_4 may be restricted to the paraconid and metaconid.
6. The lower carnassial (M_1) is serrated and is broadly concave on the medial surface rather than flat or shallowly concave.
7. M_1 is proportionately broader buccolingually than P_4. The ratio is 3:2 (14.0:9.3 mm) in the Cita Canyon (WT 1238) and 4:3 (12.7:9.1 mm) in the Friesenhahn Cave *H. serum* (TMM 933-3231).
8. The tympanohyal pit and stylomastoid foramen are subequal. These structures are separated by a distance equal to the diameter of the foramen and set in a transverse line, rather than separated by a greater distance and with

the tympanohyal pit lying anterior to the stylomastoid foramen at an angle of 45° to the midline.

9. The infraorbital canal is dorsal to the mesial root (pararadix) of P^4 rather than between the mesial and distal roots.

These differences may not remain diagnostic as more specimens become available, but they give bases for comparisons with the Eurasian Pontian-to-Villafranchian sabretooths in which homothere characters are present. Considerations of descriptions and illustrations of homotheres in the literature (e.g., Zdansky, 1924; Schaub, 1934; Teilhard and Piveteau, 1930; Teilhard and Leroy, 1945; Teilhard, 1939; de Bonis, 1976) show that there was a gradual evolution in the specialization of the carnassial functions of P^4 and M_1 from late Miocene to late Pleistocene times. Variation from the typical condition of the dentition for any one time may be expected, so that the degree of modification of the dentition of a North American homothere provides only a rough check on its synchroneity with the Eurasian sequence, where the number of extensively preserved specimens is also not great.

The conditions of the protocone and the mesial margin of the sabre are unknown in the Cita Canyon homothere, but the presence of a protoradix suggests either a vestigial cone or only a supporting root. The sabres were probably serrated on both edges as this is the normal condition. P^2 is absent, P^3 is double-rooted or may be present and variably developed or absent, and M^1 as represented by an alveolus is small and transversely elongated. This places the Cita Canyon homothere intermediate in its specialization between the Chinese Pontian (late Miocene) *Machairodus palanderi* (including *M. tingii*) and the late Pleistocene *Homotherium ultimum,* and at a stage of evolution comparable to that of *H.* cf. *crenatidens, M. nihowanensis, M. inexpectatus*, or *M. maximiliani*. In Europe a similar evolutionary stage is described for *H. nestianum* (*sic, H. nestianus*) from Perrier (Rocca Negra), France, by de Bonis (1976) from the late Villafranchian (Plio-Pleistocene Boundary).

The variability of the presence or absence and development of P^3, the protocone on P^4, the transversely elongate or styliform crown of M^1, and serrations on the cheek teeth are not known for homotheres. In most deposits carnivores are relatively rare, and in all occurrences of homotheres only two or three specimens are usually recovered, often incomplete. It is also likely that P^3 might reappear as an atavism even in otherwise highly evolved populations if the postcanine diastema could accommodate it. Moreover, the protocone on P^4 might be less likely to reappear because of the requirement that the carnassial occlusion be unhindered, and the protoradix might be variable in expression long after the protocone had been lost or reduced to a shallow style on the lingual face of the carnassial blade. The protoradix might provide some transverse stability to the carnassial under shearing stress but might be partly dependent on the thickness of the dentary at that point, as homothere dentaries are thinner than those of smilodonts. The conformation of the crown of M^1 also might be variable, in that its presence as an oblique blade distal to the upper carnassial does not always occur in *Smilodon*.

In the mandible, P_3 is separated from P_4 in *M. nihowanensis* and *H. nestianum* but is close to P_4 in *H. ultimum* or *H. serum*. The right dentary from Cita Canyon (WT 1238) preserves no P_3, although it was probably present. The Cita Canyon homothere is most similar to the Villafranchian specimens from China known as *H.* cf. *crenatidens, M. nihowanensis, M. inexpectatus,* and *M. maximiliani,* and especially *M. nihowanensis.* But the variation within this group of species suggests that the Villafranchian taxa constitute a record of evolving populations, with *H.* cf. *crenatidens* and *M. nihowanensis* representing conservative, and *M. inexpectatus* and *M. maximiliani* progressive, specimens. Of these names, *H. crenatidens* Fabrini, 1890 has priority. Mawby (1965:584) remarked on the "many similarities between *Homotherium crenatidens* and *Ischyrosmilus johnstoni*. . . . The dentitions are similar, with relatively short, flattened sabres, and high, narrow carnassials. There are numerous points of resemblance in the skull, including the form of the mastoid process, the shape of the bulla, the keel and depressions of the basioccipital and the division of the sagittal crest."

The homothere specimens from Cita Canyon, Texas, described by Mawby (1965) under the name of *Ischyrosmilus johnstoni,* are here referred to *Homotherium crenatidens,* and the Chinese species known as *Machairodus (Megantereon) nihowanensis, M. inexpectatus*, and *M. maximiliani* are also referred to *H. crenatidens* Fabrini, 1890, with the Chinese species recognized as junior synonyms of *H. crenatidens*.

THE STATUS OF *MACHAERODUS GRACILIS* AND THE SPECIES OF *ISCHYROSMILUS*

All characteristics given by Merriam for species of the genus *Ischyrosmilus,* except variation in size, are descriptive and accurately diagnostic of the Port Kennedy *Smilodon gracilis* specimens. When measurements of Merriam's type specimens of *I. ischyrus* (UCMP 8140) and *I. idahoensis* (UCMP 22343) and *I. crusafonti* (Schultz and Martin, 1970) are compared with those for the Port Kennedy sabretooth (Table 4), in no case is there sufficient disparity for a single identity to be unlikely. While in general the measurements for *I. idahoensis* and *I. johnstoni* are greater than those of the Port Kennedy and Florida materials, those of *I. ischyrus* and *I. crusafonti* are

within the ranges of variation that might be expected in an extensive series.

The Port Kennedy sabretooth, originally described as *Machaerodus gracilis* and *M. mercerii*, or referred to as *Smilodontopsis gracilis* and *Smilodon gracilis* in subsequent literature, is therefore congeneric with taxa described within the genus *Ischyrosmilus* Merriam, 1918. The acceptance of five species in this genus, founded on six occurrences for *I. gracilis* (Port Kennedy Caverns, Pennsylvania, Sante Fe I, Inglis IA, Haile XVA, Bass Point Waterway I, and El Jobean Pit, Florida), and single occurrences for *I. ischyrus* (Asphalto, California), *I. idahoensis* (Froman Ferry, Idaho), and *I. crusafonti* (Dan Bowman Ranch, Nebraska), with two possible individuals of *I. johnstoni* (Cita Canyon, Texas), appears unlikely. The four smaller species (Table 4) constitute a single taxon on the evidence of morphology and size, and the two larger specimens may represent either a second species or larger variants attributable to sexual dimorphism or simple size variation. Moreover, the extremes of measurements for *S. californicus* are similar to those observable in *Ischyrosmilus* (Tables 3–5). Size variation in *Ischyrosmilus* may thus reflect either simple variation or sexual dimorphism, if all the specimens were contemporaneous. However, Evernden et al. (1964) and Mawby (1965) considered that *Ischyrosmilus* was restricted to Blancan faunas. All known specimens derive from Blancan or Irvingtonian deposits, with those of *I. idahoensis, I. johnstoni*, and *I. crusafonti* being later (early Pleistocene) and others earlier (late Pliocene or earliest Pleistocene). It is thus possible that *I. idahoensis, I. johnstoni,* and *I. crusafonti* represent somewhat later populations in which the average size and massiveness were greater than in the better-known earlier populations.

The genus *Ischyrosmilus* Merriam, 1918 must take precedence over North American names, in that *Smilodon* Lund, 1842 is not available, *Smilodontopsis* Brown, 1908 is a synonym of *Smilodon,* and *Homotherium* Fabrini, 1890 does not apply to any of the type specimens. Cope (1880) originally described the Port Kennedy materials as *Machaerodus gracilis* and *Uncia mercerii* (1895) or *M. mercerii* (1899). *Machaerodus* is a variant of *Machairodus* Kaup, 1833, which under Article 33(b) of the International Code of Zoological Nomenclature (Stoll et al., 1961:37) is an "incorrect subsequent spelling" and "has no status in nomenclature and therefore does not enter into homonymy and cannot be used as a replacement name."

The correct name for the Port Kennedy sabretooth is *Ischyrosmilus gracilis* (Cope, 1880), and *Machaerodus* is therefore neither a synonym nor available as a replacement name. The smaller species of *Ischyrosmilus* described by Merriam, *Ischyrosmilus ischyrus* (Merriam, 1905) (= *Machaerodus ischyrus* Merriam, 1905), and *I. crusafonti* Schultz and Martin, 1970 (but not *I. osborni* Merriam, 1919) are synonyms of *Ischyrosmilus gracilis* (Cope, 1880), including *Machaerodus (Smilodon) mercerii* Cope, 1899, but the genotype is *Ischyrosmilus ischyrus,* as Merriam (1918) founded the genus on the specimen previously described (1905) as *Machaerodus? ischyrus*. The status of *Ischyrosmilus idahoensis* Merriam, 1918 (including *I. johnstoni* Mawby, 1965) is dependent on the significance of greater size. At present, because of the paucity of specimens, and because no evidence exists to distinguish *I. idahoensis* from the *I. gracilis* specimens on criteria that are independent of possible sexual or normal size variation, it is wise to consider *I. idahoensis* synonymous with *I. gracilis*.

The geological dates given for the *Ischyrosmilus* specimens are late Pliocene for *I. ischyrus* and *I. johnstoni,* late Pliocene or early Pleistocene (Blancan or Irvingtonian) for the Florida specimens of *I. gracilis* and for *I. idahoensis,* early Pleistocene for *I. crusafonti,* and Pleistocene for *I. gracilis* (including *I. mercerii*). Actual age of the Port Kennedy Cavern deposits is probably less certain than that of any of the other *Ischyrosmilus*-yielding deposits (Kurtén and Anderson, 1980), as stratigraphic evidence within caves can be misleading, and the associated faunal remains either inadequate for dating or dischronous.

Hibbard (1955:94) considered the Port Kennedy microtine rodents "more advanced than those occurring in the earlier Pleistocene faunas such as the Hagerman of Idaho, the Sand Draw of Nebraska, the Deer Park and Sanders of Kansas." Latest ages for these faunas are: Hagerman 3.7 My, Sand Draw 3.1–2.8 My, Deer Park 3.1–3.0 My, and Sanders 2.8 My, approximately, and all represent Blancan faunal assemblages (Lundelius et al., in press). It is likely that at least part of the Port Kennedy fauna dates from the later part of the Blancan, or from the early Irvingtonian land mammal ages, and that an early Pleistocene date is probable.

Evolutionary trends in *Ischyrosmilus* appear to be from a smaller and more gracile form toward a larger and more robust one. The temporal range of the genus may be restated as early Pliocene to early Pleistocene in North America, and its distribution to include the areas of the present Great Plains, Idaho, California, Florida, Pennsylvania, and northwards, possibly as far as the Canadian prairies, in a pattern reminiscent of that of its later descendant *Smilodon*. At present the known sample is too small to permit suggestions of regional variants, although the specimens from Florida are the most numerous and indicate considerable variation in individual size.

RELATIONSHIPS OF THE GENUS *ISCHYROSMILUS*

The first description of specimens of *Ischyrosmilus* from

the Port Kennedy Fissure, Pennsylvania, and Asphalto, California, were within the genus *Machaerodus* (Cope, 1880; Merriam, 1905), and both Cope and Merriam commented on resemblances to Eurasian species of *Machairodus*. Mawby (1965:584) presented an opposing view: "It is likely that direct comparison of *I. johnstoni* with specimens of *H. crenatidens* would show the two to be congeneric." He added that "it seems best to retain the name *Ischyrosmilus* for the early Pleistocene homotheres of North America." However, this opinion was probably influenced by the homothere characters of the skull and hind limb of the Cita Canyon sabretooth specimens.

Taxonomic confusion has obscured the systematic relationships of Pliocene and Pleistocene machairodonts of the Holarctic and Ethiopian regions in the past. They differ from *Felis* in the presence of well-developed mastoid processes, reduced coronoid processes on the mandible, elongated and massive mandibular symphyses, elongated and hypsodont (sabre-like or dagger-like) upper canines, premolars reduced both in number and in effective shearing length, and strong and trenchant carnassials. Their bodies were strong to massive, the tail apparently always short, as in *Lynx,* and the limbs strong with powerful claws. All were large, similar in size to the lion (*Felis leo*), leopard (*F. pardus*), or jaguar (*F. onca*), and readily distinct from these extant large cats on morphological differences.

Piveteau (1961:786) avoided some of the taxonomic problems within the Machairodontinae, referred to them as the "Machairodontoid Lineage", and commented "Il y a toujours eu une grande confusion dans la nomenclature de ces formes; d'abord dans les désignations spécifiques quand elles étaient toutes rangées sous la dénomination de *Machairodus;* ensuite dans les désignations génériques quand le genre initial fut à son tour découpé, parfois d'une façon abusive et sans justification suffisante, en de nombreux autres genres."

Croizet and Jobert (1828) described *Megantereon* from the Villafranchian of Senèze, France, and Kaup (1833) described *Machairodus* from the Pontian of Eppelsheim, Germany. These two genera represent two already separate lineages of sabretooths, recognized by Kurtén (1963) as the tribes Smilodontini (dirk sabretooths) and Homotheriini (scimitar sabretooths), respectively, but named from the middle and late Pleistocene genera *Smilodon* and *Homotherium*.

Megantereon is known from Eurasia and Africa and has been reported from the Blancan of North America (Schultz and Martin, 1970; Kurtén and Anderson, 1980) and also from the late Hemphillian (Berta and Galiano, 1983). It was as big as a cougar or panther and increased in size through time. Its dentition is characterized by strongly hypsodont upper canines that are slim and dirk-like and lack serrations on their margins (Figs. 9A,B, 12A). The upper third premolars, P^3's, are somewhat reduced but functional. The upper carnassials, P^4's, possess single parastyles, paracones, metacone blades, and strong protocones, and the upper molars are transversely elongate and reduced. The lower carnassials, M_1's, lack evidence of metaconids or talonids, except as cingula. The sabres, C^1's, occlude posteriorly free of the lower canines and within the lower diastemata, and functional P_3's are present. The skull is massive, with a short muzzle, convex dorsal outline, low nasals, and flaring nuchal crest. The glenoid process extends to the level of the external auditory meatus and down to, or below, the occlusal plane. The mastoid process is large and lies posterior to the meatus and bulla. The mandibular symphysis is strong, vertical, with well-developed genial flanges almost double the depth of the dentary in the diastema.

Machairodus is known from the Pontian of Eurasia, and from Africa, and is reported from North America by Martin and Schultz (1975, Hemphillian and Kimballian), Martin (1980, Hemphillian or late Clarendonian), and Harrison (1983, late Hemphillian). Kurtén and Anderson (1980) did not recognize this genus in North America but suggested that *Homotherium* (Fig. 11) might derive from that genus. *Machairodus* was the size of a lion. Its dentition is characterized by a less hypsodont scimitar-like canine that is broader mesiodistally than that of *Megantereon,* proportionately more compressed buccolingually, and strongly serrated on both edges. The sabre occludes past the lower canine's distal edge, with the distobuccal ridge on the lower canine serrated, and the incisors set in a rounded arc. The second upper premolars are single-rooted and reduced, if present. The second lower premolars are larger and two-rooted with differentiated crowns, and the third and fourth premolars may have serrated margins. The upper carnassials have variably developed protocones, integral with the side of the paracone, strong shearing blades, and double parastyles, and the upper molars are oval or round, but not usually transversely elongate. The lower carnassial is trenchant and may have vestigial metaconids or talonids.

The skull of *Machairodus* is low-crowned, with a less convex dorsal outline than *Megantereon,* the nasals are higher and the muzzle longer, the infraorbital canal is oval in section, and its diameter is less than 40 per cent of the maximum orbital diameter, the tympanic bullae are not highly inflated, the mastoid process is massive and rugose, and the glenoid process extends to the occlusal plane. The mandibular symphysis is inclined at an obtuse angle to the axis of the horizontal ramus, and the genial flanges are smaller than in *Megantereon*. The limbs are longer and the claws less massive.

The salient points in which *Megantereon* differs from *Machairodus* are the more dirk-like sabres that lack serrations and which occlude distal to the unserrated lower

canines, unserrated incisors, distinct protocones and double parastyles on the upper carnassials, the transversely elongated upper molar, the absence of a rudimentary upper second premolar, the vertical symphysis with the large genial flanges, the developed lower third premolar, the lower nasals and the convex outline of the skull, the inflated bullae, and the shorter and more massive limbs and claws.

Ischyrosmilus is similar to *Megantereon* in the lower nasals, probably a convex dorsal outline to the skull, the proportions and section of the sabres and their occlusion entirely posterior to the lower canines, the simple parastyle and the occasional presence of a protocone on the upper carnassial, the vertical orientation of the mandibular symphysis with sharp genial flanges, and the transverse alignment of the incisors and lower canine. The mastoid and glenoid processes are ventrally elongated and approach each other but do not almost touch, as in *Smilodon*.

Smilodon (Fig. 12B) is derived from the *Megantereon* condition by further emphasis on the hypsodonty of the sabre, reduction of the third upper premolars, the almost completed loss of the third lower premolars, and greater development of the sagittal and nuchal crests. *Smilodon* also has serrations on the margins of the upper canines and on the distobuccal ridge of the lower canine, but these are less well developed than in *Machairodus* or *Homotherium* and are different in form. It had newly evolved an elongated mastoid process that extends anteriorly and ventrally to below the level of the external auditory meatus and to within 1 or 2 mm of the postglenoid process.

Ischyrosmilus gracilis (Fig. 1) represents an intermediate transition towards that of *Smilodon* in the reduction of the third lower premolars, development of fine serrations on the canines and other teeth, and an elongate mastoid process that approaches the postglenoid surface to within 5 mm.

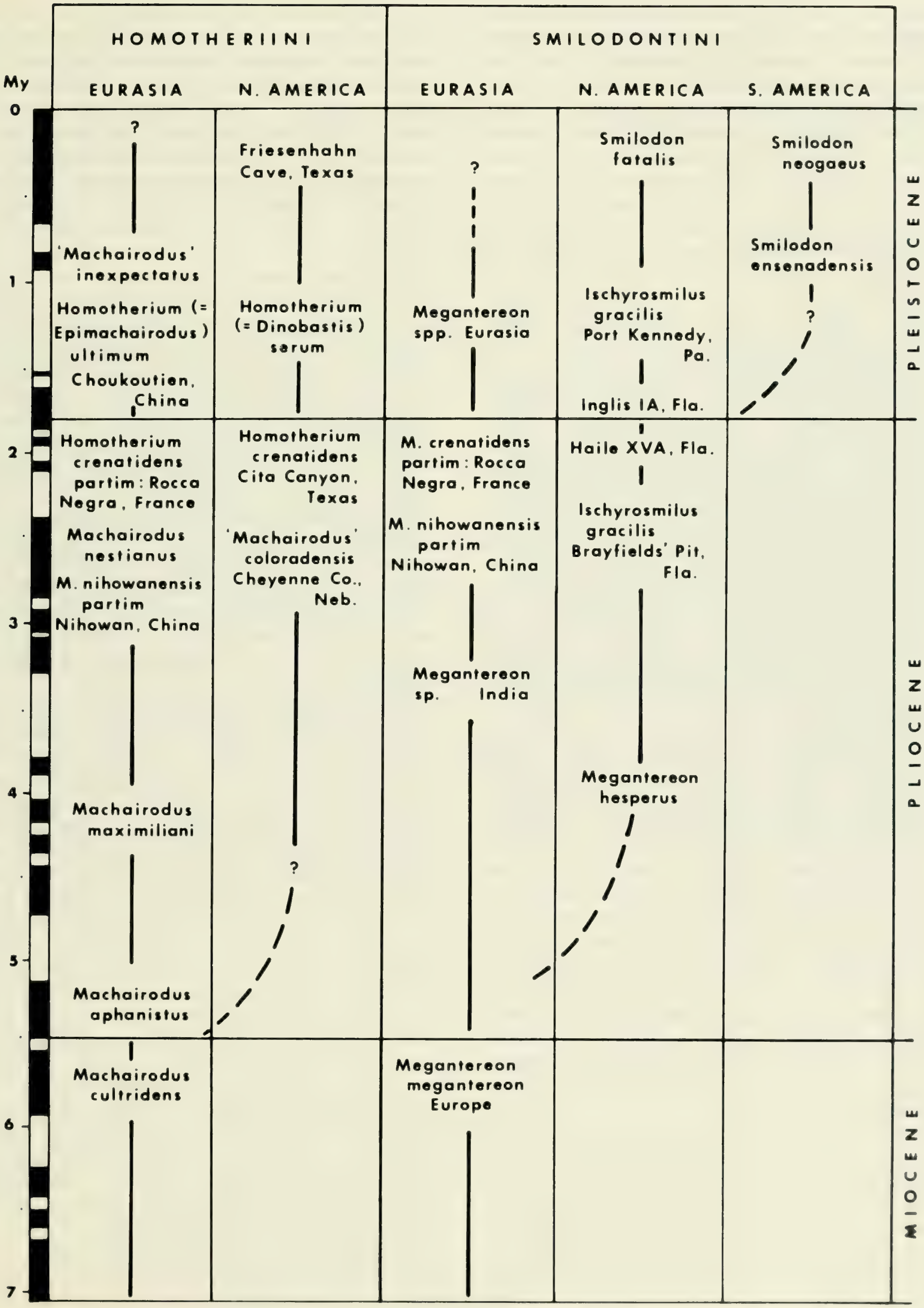
The Neogene machairodonts therefore represent two distinct lineages which had a common Eurasian origin during the early or middle Miocene (Fig. 13). The separate lineages, begun by *Machairodus* and *Megantereon,* were well established by the early Pliocene and widespread across Eurasia and Africa. By Blancan or Villafranchian times, the *Machairodus* lineage had evolved from the level exemplified by *M. aphanistus* to that of *Homotherium* (= *Machairodus) crenatidens* and was trending towards the advanced level shown in *Homotherium* (= *Epimachairodus) ultimum* or *H. serum*. The changes involved in the evolution of *Homotherium* from *Machairodus* appear to have been so gradual, and the variations in the morphological characters within coeval populations so great, that the examples of the populations available do not provide characters to distinguish the grades, nor does the fossil record provide convenient accidental gaps by which to separate genera or species.

Megantereon is known from the earliest Villafranchian in Europe, possibly from the Pliocene of India, and became extinct in Europe at the end of the Villafranchian but survived in Africa and Asia into the middle Pleistocene. By early Pliocene times the lineage may be represented in North America by *Megantereon hesperus,* from which a new species, *Ischyrosmilus gracilis,* may have arisen by late early or middle Pliocene times. This species later differentiated into the large and successful New World sabretooth *Smilodon,* known from middle Pleistocene times to after the retreat of the Wisconsin ice and from both North and South America. The smilodont lineage paralleled the homothere in the development of serrations on the teeth, albeit different in detail, and in the reduction of P_3's. This lineage introduced a new conformation within the Machairodontinae in the close apposition of the mastoid and postglenoid processes in response to a variant mechanism for closing the jaw. Similar modifications for the areas supporting the glenoid had occurred earlier in the Oligocene *Eusmilus* and middle Miocene (Clarendonian) *Barbourofelis*.

Kurtén (1963), Slaughter (1963), and Webb (1974) referred the Port Kennedy specimens to *Smilodon,* and Martin (1980) referred them to *Megantereon*. *Ischyrosmilus gracilis* can be distinguished from both *Megantereon* and *Smilodon* by size and morphologies which show interesting intermediate evolutionary stages. The evolutionary changes that took place in the smilodonts were greater than those in the homotheres, which effectively experienced only refining of already-evolved structures. The smilodonts continued to reduce the premaxillary dentition, separately acquired serrations on the canines, and altered the conformation of the auditory region. *Ischyrosmilus* is as distinct from *Megantereon* as it is from *Smilodon,* and thus it is a morphospecific taxon which, because it may be recognized qualitatively and without recourse to fine measurements, probably deserves generic rank. This may only be confirmed by the discovery of additional specimens.

Fig. 13. Selected occurrences of Homotheriini and Smilodontini in Eurasia and the Americas, arranged as lineages.

Times of the original migrations from Eurasia to North America or from North America to South America are approximate, as are temporal positionings of the occurrences. Later exchange migrations across the Bering Strait in either direction or southwards across the Panamanian Isthmus after the original immigrations are not indicated. Time-Scale in 10^6 years (My) and Magnetic Reversal Scale in black (normal polarity) and white (reversed polarity) column.


HOMOTHERIINI
SMILODONTINI
My
EURASIA
N. AMERICA
EURASIA
N. AMERICA
S. AMERICA
0
1
2
3
4
5
6
7
?
'Machairodus' inexpectatus
Homotherium (= Epimachairodus) ultimum
Choukoutien, China
Homotherium crenatidens partim: Rocca Negra, France
Machairodus nestianus
M. nihowanensis partim
Nihowan, China
Machairodus maximiliani
Machairodus aphanistus
Machairodus cultridens
Friesenhahn Cave, Texas
Homotherium (= Dinobastis) serum
Homotherium crenatidens
Cita Canyon, Texas
'Machairodus' coloradensis
Cheyenne Co., Neb.
?
?
Megantereon spp. Eurasia
M. crenatidens partim: Rocca Negra, France
M. nihowanensis partim
Nihowan, China
Megantereon sp. India
Megantereon megantereon Europe
Smilodon fatalis
Ischyrosmilus gracilis
Port Kennedy, Pa.
Inglis IA, Fla.
Haile XVA, Fla.
Ischyrosmilus gracilis
Brayfields' Pit, Fla.
Megantereon hesperus
Smilodon neogaeus
Smilodon ensenadensis
?
PLEISTOCENE
PLIOCENE
MIOCENE

Confusion has long existed over the identification of sabretooths within the *Machairodus-Epimachairodus-Homotherium* (including *Dinobastis*) and the *Megantereon-Ischyrosmilus-Smilodon* lineages. Schaub (1934) discussed this confusion and the taxonomic problems of separating *Machairodus* or *Epimachairodus* (= *Homotherium*) from *Megantereon* in the early Pliocene. The inclusion by Teilhard and Piveteau (1930) within *Machairodus nihowanensis* of specimens from the late Pliocene of Nihowan, China, that are assignable to both *Epimachairodus crenatidens* and *Megantereon*, and the inclusion by Bielawski (1905) within *Machairodus nestianus* of specimens from the late Pliocene of Rocca Negra, Perrier, France, assignable to both *Epimachairodus crenatidens* and *Megantereon*, only added to this confusion.

Mawby's (1965) inclusion of both a homothere (*Homotherium*) and a smilodont (*Ischyrosmilus*) within *Ischyrosmilus johnstoni* has already been discussed. De Bonis (1976) reviewed the machairodonts from Rocca Negra, France, reconsidered the skull described by Schaub (1934), and identified it to *Machairodus nestianus* as *Homotherium nestianus (sic)* from the Pliocene-Pleistocene boundary (middle Villafranchian). He (1976:17) suggested that the differences between *H. nestianum* and *H. crenatidens* are insufficient for a specific separation. Schaub (1934:405) had already suggested, after studying the same skull from Rocca Negra, that the distinctive specific characters invoked by Fabrini (1890) had value only at the level of individual or sexual differences.

De Bonis (1976) considered that Meade (1961) included within *Dinobastis serus* the two crania TMM 933-3582 and -3231 of which TMM 933-3231 represents *Ischyrosmilus*. He stated (1976:20) that in TMM 933-3231, C^1, "la canine supérieure est proportionnellement plus longue et semble plus finement crénelée, la troisième prémolaire supérieure est plus longue, la carnassière est plus courte relativement à la taille de l'animal, le profil supérieur du crâne est plus bombé et surtout l'apophyse glénoïde est plus longue et la cavité glénoïde se trouve nettement au-dessous du méat auditif externe." Cranium TMM 933-3231 is an adult with fully erupted sabres, whereas TMM 933-3582 has sabres deeply set within the alveoli, probably as a result of postmortem compaction into the alveoli. The dorsal outline of TMM 933-3231 appears more rounded because its nasals are not preserved.

P^3's cannot be compared as none is extant in TMM 933-3582. The right P^4 of TMM 933-3582 differs by less than 1 mm from the left P^4 of TMM 933-3231 (37.6 × 12.7 versus 38.6 × 12.0 mm for mesiodistal and buccolingual diameters) and thus is longer, although the total lengths of the two skulls show TMM 933-3231 to be longer (362 versus 324 mm for the premaxillary-condylar length). Moreover, the level of the glenoid surface in TMM 933-3582 relative to the external auditory meatus is the result of a combination of minor distortions of the fossil and the artistry in Meade's (1961, fig. 1) illustration. De Bonis's (1976) contention that *Ischyrosmilus* is also present in the Friesenhahn Cave materials assigned to *Dinobastis serus* by Meade is erroneous and appears to be based on his misinterpretation of Meade's illustrations and the possible influence of Mawby's (1965) identification of a homothere skull as the smilodont *Ischyrosmilus johnstoni*.

Martin and Schultz (1975) described and figured *Machairodus* cf. *coloradensis* from the Kimball Formation (Upper Pliocene) of Cheyenne County, Nebraska, and from the upper part of the Ash Hollow Formation (Pliocene, Hemphillian) of Sherman County, Nebraska, the latter as a new subspecies, *M. coloradensis tanneri*. They concluded (1975:55) that their "new subspecies demonstrates evolutionary trends which seem to be leading to *Ischyrosmilus* from the lower Quaternary (Blancan)." It appears that they also relied on Mawby's (1965) description of *Ischyrosmilus johnstoni* in their evaluation of the relationships of their specimens and in their concluding remarks. Their two *Machairodus* are typical of the early stages of the genus sensu lato, probably at the level of *Homotherium crenatidens* or *H. palanderi*, and show none of the derived characters that typify the *Ischyrosmilus* stage in the *Megantereon* to *Smilodon* lineage.

Martin (1980:149–150) compounded the Martin and Schultz (1975) error when he stated: "Along with *Megantereon*, we find a long-legged, short-tailed scimitar-toothed cat (*Homotherium*) occurring in Eurasia, Africa and North America. The North American form has been described as *Ischyrosmilus*, as I have generally supported the separation of the two genera (Schultz and Martin, 1970; Martin and Schultz, 1975), but I now regard them as congeneric. A related genus, *Dinobastis*, has a cruciate sulcus on the brain (based on the McPherson Equus Beds specimens of *Dinobastis*), and I regard *Homotherium* and *Dinobastis* as felids." Martin's first two sentences state that *Homotherium* and *Ischyrosmilus* are congeneric. His third sentence places *Dinobastis* (= *Homotherium*) in the Felidae. All the genera named are Felidae, but *Ischyrosmilus* belongs to the tribe Smilodontini and *Homotherium* and *Dinobastis* to the tribe Homotheriini, and although the latter two may be congeneric, *Homotherium* is not a possible congener of *Ischyrosmilus*. Last, to my knowledge, the scimitar cats (genus *Homotherium*) have never been intentionally placed in *Ischyrosmilus*, except by Martin (1980), probably because their dental and basicranial characters are essentially dissimilar. However, Mawby (1965) referred *Ischyrosmilus* to the Homotheriini *fide* Kurtén

(1963:98) where "*Ischyrosmilus?*" is referred to as a homothere.

The confusion that has existed concerning identification of the homothere and smilodont lineages still exists, despite the diagnoses and efforts of previous workers (e.g., Pilgrim, 1931; Schaub, 1925, 1934; Kurtén, 1963; Churcher, 1966; Kurtén and Anderson, 1980). It is necessary to have a clear concept of the two functional conformations and to decide to which lineage a specimen belongs on the basis of a knowledge of their morphological differences before attempting to place a name on the specimen. Some of the confusion appears to have occurred because of reversals of this procedure, and the inclusion of specimens from both coeval and sympatric but different lineages within a single taxon.

Conclusions

The names that have been applied to the gracile sabretooth *Ischyrosmilus gracilis* are: *Machaerodus (Smilodon) gracilis* Cope, 1880; *Smilodon gracilis* Cope, 1895; *Uncia mercerii* Cope, 1895; *Machaerodus (Smilodon) mercerii* Cope, 1899; *Smilodon (Smilodontopsis) gracilis* Merriam and Stock, 1932; *Machaerodus? ischyrus* Merriam, 1905; *Ischyrosmilus? idahoensis* Merriam, 1918; *Ischyrosmilus ischyrus* Merriam, 1918; *I. johnstoni* Mawby, 1965; *I. crusafonti* Schultz and Martin, 1970; and *M(eganterion) gracilus* Martin, 1980. These names have been applied by various authors (e.g., Slaughter, 1963; Kurtén, 1965; Webb, 1974; Robertson, 1976; and Kurtén and Anderson, 1980) in different ways to refer to specimens included within these taxa.

Machaerodus Cope, 1880 is an invalid variant of *Machairodus* Kaup, 1833. The genus *Smilodontopsis* Brown, 1908 was first applied to true *Smilodon* and thus is a junior synonym of *Smilodon* Lund, 1842 and therefore unavailable. *Smilodontopsis troglodytes* and *S. conardi* are therefore true *Smilodon*.

Ischyrosmilus gracilis (Cope, 1880) is the first described species of the genus *Ischyrosmilus* Merriam, 1918, of which the type species is *Ischyrosmilus ischyrus* Merriam, 1917, originally described as *Machaerodus? ischyrus* Merriam, 1905. The genus *Ischyrosmilus* comprises the species *I. gracilis* (Cope, 1880), with *I. mercerii* (Cope, 1895), *I. ischyrus* (Merriam, 1905), and *I. crusafonti* Schultz and Martin, 1970 as conspecific synonyms. Larger specimens described as *I. idahoensis* Merriam, 1918 and *I. johnstoni* Mawby, 1965 are probably only sexually dimorphic or morphological variants of *I. gracilis* but may constitute a later taxon for which the name *I. idahoensis* Merriam, 1918 is available.

Ischyrosmilus is intermediate between *Megantereon* and *Smilodon* in characters of its dentition and jaw articulation. It evolved from an immigrant *Megantereon*, possibly *M. hesperus* from the early Pliocene of North America, is found in deposits of early or middle Pliocene to early Pleistocene ages (Blancan and Irvingtonian faunal ages), and probably evolved into *Smilodon* by middle Pleistocene times. *Smilodon* became extinct probably in early Holocene times. *Ischyrosmilus* belongs to the tribe Smilodontini and possesses the dirk-like sabres, the ventrally extended glenoid process, the reduced lower third premolar, and other characters typical of the tribe.

Acknowledgements

This report stems from my interest in the genus *Smilodon* sensu lato and from conversations with many vertebrate palaeontologists about it. I have to thank the curators, assistants, and students in many North American museums who since 1965 have assisted me, allowed me to examine and borrow specimens, and discussed the anatomy and phylogenies of sabretooths.

I am particularly indebted to Dr. Björn Kurtén of the University of Helsinki with whom I have corresponded through the years about *Smilodon*, *Dinobastis*, and *Ischyrosmilus johnstoni;* Dr. David Gillette, then of the Academy of Natural Sciences, Philadelphia, who allowed me to examine the type materials of *Smilodontopsis troglodytes*, *S. conardi*, and *S. mooreheadi;* Dr. Theodore Downs of the Los Angeles County Museum, Los Angeles, who allowed me to examine the collections of *Smilodon californicus* from Rancho La Brea; Dr. Ernest L. Lundelius, Jr., of the University of Texas and Texas Memorial Museum, Austin, who allowed me to study and measure the collections of *Homotherium serum* from the Friesenhahn Cave; and Dr. S. David Webb of the University of Florida and Florida State Museum, Gainesville, who allowed me to examine and refer to the cast of the Inglis IA dentary assigned to *Smilodon gracilis*.

Dr. Annalisa Berta, who is currently studying the Florida sabretooths, discussed the phylogeny and history of the Pleistocene sabretooths, read and commented on my paper in draft, and allowed me to read a draft of her paper, "The sabrecat *Smilodon gracilis* from Florida and a discussion of its relationships". Dr. Kurtén, Dr. John E. Mawby of Deep Springs College, California, Dr. Thomas S. Parsons of the University of Toronto, and Dr. Christopher McGowan of the Royal Ontario Museum, Toronto, read drafts of this paper and offered critical advice. Miss Airlie Armstrong and Miss Judy Hann, my technical assistants, typed the manuscript, and, with Dr. James A. Burns, then of the Department of Zoology, University of Toronto, now of the Provincial Museum of Alberta, Edmonton, checked for inconsistencies and errors with great good humour. Mr. John Glover of the Faculty of Arts and Science, University of Toronto, Photographic Facility, produced the photographs used for the plates and those from which many of the line diagrams were made efficiently and quickly.

Last, and most important, I thank Mr. and Mrs. William Brayfield of El Jobean, Florida, and Dr. A. Gordon Edmund of the Royal Ontario Museum, who collected at the Bass Point Waterway and El Jobean Pit sites and allowed me to incorporate their new materials into this report. Without their interest, patience, and support, this paper would have lacked the new data by which many of the conclusions are substantiated.

Table 1 **Measurements of the dental holotypes of *Smilodontopsis troglodytes* and *S. conardi* and of associated dental elements assigned to *Smilodon?* from the Conard Fissure, Arkansas.**

Measurements taken by the author. Size ranges for similar dimensions of *Smilodon* from Rancho La Brea, California, and Talara, Peru, are derived from Merriam and Stock (1932) and from measurements by the author. Measurements are in millimetres. "e" indicates an estimation, "w" that the crown of the tooth is worn, parentheses an incomplete dimension, and "-" that the dimension is unmeasurable.

Elements and Dimensions	*Smilodontopsis troglodytes* Conard Fissure, Arkansas AMNH 11786	*Smilodontopsis conardi* Conard Fissure, Arkansas AMNH 11790	*Smilodon?* Conard Fissure, Arkansas AMNH 11787	Size ranges for *Smilodon* derived from Rancho La Brea, California, and Talara, Peru (N) = sample size
I^1 Mesiodistal diameter	8.0		7.1	7.6–5.0 (26)
Buccolingual diameter	9.6		8.9	12.7–8.8 (44)
Crown height	16.4		13.9	18.3e–11.6 (35)
Root length	31.5		-	
Total length	45.2		-	45.8e–35.0 (4)
I^2 Mesiodistal diameter		9.7		9.7–7.3 (25)
Buccolingual diameter		12.6		14.6–10.1 (48)
Crown height		20.3		22.1–14.2e (33)
Total length		46.9		48.2–40.0 (6)
C^1 Mesiodistal diameter		(31.3)		51.0e–36.0 (42)
Buccolingual diameter		(13.8)		24.1–15.3 (38)
Mesial crown height		(100.3)		141.4–123.0e (15)
Distal crown height		(97.6)		151.7–128.3 (14)
Length of fragment	37.3	100.3	27.1	
P^4 Mesiodistal diameter	37.5	37.2	-	46.3–33.4 (48)
Buccolingual diameter	14.7	15.6	14.7e	18.8–11.1 (49)
Crown height over parastyle	8.9	8.3	7.3	14.1e–absent (24)
Crown height over paraconule	17.9	-	16.9e	11.9–8.7 (18)
Crown height over paracone	-	19.6	-	27.3–17.4 (29)
Crown height over protocone	absent	6.2	6.2e	24.9–20.6 (19)
Crown height metacone	17.1e	15.5	-	21.6w–16.3 (36)
Length of metacone blade	15.2	15.4	-	17.6–11.5 (27)
P_3 Mesiodistal diameter			10.1, 9.7	10.2–6.5 (2)
Buccolingual diameter			6.8, 7.0	7.1–5.7 (2)
Crown height			7.4, 7.7	8.3–5.8 (2)
Total length			25.4, -	

Table 2 Measurements of postcranial elements (except phalanges) of the holotypes of *Smilodontopsis troglodytes* and *S. conardi*, and of the associated postcranial elements assigned to *Smilodon?*, from the Conard Fissure, Arkansas.

Size ranges for similar dimensions of *Smilodon* from Rancho La Brea, California, and Talara, Peru, are derived from Merriam and Stock (1932) and from measurements by the author. Measurements are in millimetres. "e" indicates an estimation and "-" that the dimension is unmeasurable.

Elements and Dimensions	*Smilodontopsis troglodytes* Conard Fissure, Arkansas AMNH 11786			*Smilodontopsis conardi* Conard Fissure, Arkansas AMNH 11792	*Smilodon?* Conard Fissure, Arkansas AMNH 11787	Size ranges for *Smilodon* derived from Rancho La Brea, California, and Talara, Peru (N) = sample size
Dentary						
Buccolingual diameter of condyle	40.6					58.2–39.3 (44)
Dorsoventral diameter of condyle	16.0					25.2–16.2 (43)
Lumbar Vertebrae	No. ?3	No. ?4	No. ?5			Nos. 3, 4, and 5
Length of centrum	47.7	50.2	49.2			52.4–39.4 (18)
Zygapophyseal length	59.8	63.0	-			81.9–59.0 (16)
Metapophyseal width	-	53.4e	-			71e–47.6e (16)
Postzygapophyseal width	49.0e	41.0	-			52e–32.4 (16)
Width across posterior central epiphysis	41.3	43.7	41.7			48.4–38.5 (18)
Depth of posterior central epiphysis	28.5	29.3	27.6			35,0–24.6 (18)
Height of neural spine above centrum of anterior central epiphysis	82.9	-	-			113.3–85.7 (11)
Humerus	left			right		
Maximum transverse distal diameter	86.3			77.9e		128.3–93.7 (22)
Minimum diameter of ulnar trochlear	23.6			27.3		36.0–25.2 (25)
Ulna	left			left		
Maximum anteroposterior distal diameter	33.2			33.4		46.6–31.3 (21)
Maximum transverse disatal diameter	19.3			20.2		33.8–19.1 (21)
Radius	left					
Maximum transverse distal diameter	45.3					67.3–49.4 (20)
Maximum anteroposterior distal diameter	32.4					48.2–35.6 (20)
Tibia						
Maximum transverse distal diameter				53.1		63.3–45.0 (20)
Maximum anteroposterior distal diameter				34.3		41.5–35.6 (20)
Minimum transverse diameter of shaft				32.7		33.0–25.1 (16)
Minimum anteroposterior diameter of shaft				24.5		32.2–28.9 (6)
Scapholunar (lacking pisiform facet)				left	left	
Maximum dorsopalmar depth				32.7	28.0	44.7–31.6 (17)
Maximum proximodistal diameter				24.2	21.7	35.4–25.3 (18)

Pisiform				right			
Maximum length				35.2			49.4–36.0 (21)
Greater diameter over articulations				20.1			26.8–21.4 (21)
Greater diameter of head				17.7			29.6–17.4 (21)
Maximum proximodistal diameter of head				13.2			16.3–11.4 (21)
Unciform				left	right	right	
Proximodistal diameter				27.6	24.2	27.6	34.2–23.8 (16)
Maximum dorsoplantar diameter				30.4	29.3	30.9	40.8–28.7 (16)
Maximum dorsal width				27.3	25.1	24.7	27.1–19.5 (16)
Navicular				right			
Dorsoplantar depth				41.7			48.0–27.0 (16)
Transverse diameter				28.6			37.4–28.4 (16)
Cuboid				left			
Maximum proximodistal diameter				23.6			31.4–24.7 (21)
Maximum transverse diameter				25.4			31.4–21.3 (21)
Maximum dorsoplantar depth				25.1			42.3–27.5 (21)
Calcaneum				right			
Maximum length				84.4			106.8–79.4 (22)
Maximum width over sustentaculum				48.7			54.4–40.4 (22)
Maximum width over cuboid facet				35.8			44.2–32.5 (22)
Maximum depth on lateral surface				37.5			48.9–35.1 (22)
Astragalus	right			left	right		
Maximum length	44.3			47.7	47.5		61.2–44.6 (33)
Maximum transverse diameter	42.2			48.8	45.4		61.2–46.0 (31)
Maximum diameter of neck	21.8			22.6	22.8		29.5–21.0 (31)
Maximum diameter of head	28.1			30.5	30.1		38.0–26.7 (30)
Mesocuneiform	left						
Maximum length	24.6						28.6–21.2 (5)
Transverse diameter normal to maximum length	12.9						13.2–10.9 (5)
Maximum proximodistal thickness	10.3						14.2–9.6 (5)
Ectocuneiform				right			
Maximum dorsoplantar length				37.0			48.9–25.1 (15)
Maximum proximodistal diameter				15.6			18.4–13.6 (11)
Maximum width across metatarsal facet				22.7			29.7–21.4 (15)
Metacarpalia	II	III	IV				III
	left	left	left				
Maximum length	-	100.0e	-				109.6–83.0 (25)

Table 2 (continued)

Elements and Dimensions	*Smilodontopsis troglodytes* Conard Fissure, Arkansas AMNH 11786			*Smilodontopsis conardi* Conard Fissure, Arkansas AMNH 11792	*Smilodon*? Conard Fissure, Arkansas AMNH 11787	Size ranges for *Smilodon* derived from Rancho La Brea, California, and Talara, Peru (N) = sample size
Metacarpalia (continued)	II left	III left	IV left			
Dorsoplantar depth of proximal end	-	24.0	-			29.2–22.8 (24)
Transverse diameter of shaft	-	11.7	-			20.0–13.9 (25)
Dorsoplantar diameter of shaft	-	12.5	-			16.7–12.3 (25)
Transverse diameter of distal end	20.2	19.0	21.6			24.5–20.2 (20)
Metatarsal III	III left					
Transverse diameter of shaft	13.4					18.2–14.9 (28)
Dorsoplantar diameter of shaft	12.2					16.9–12.8 (27)
Transverse diameter of distal end	22.3					26.9–20.3 (27)

Table 3 Measurements of the upper permanent dentitions and diastemata of the neotype of *Machaerodus (Smilodon) gracilis* and the holotype of *M. (S.) mercerii* and other specimens from Port Kennedy Caverns, Pennsylvania, of *Smilodon* from Rancho La Brea, California, and Talara, Peru, of "*Ischyrosmilus*" *johnstoni* from the facial portion (WT 1860) and other specimens, of the partial left sabre of *I. crusafonti* (UNSM 25503) and right sabre of *Ischyrosmilus* sp. (UNSM 1105), and of *Homotherium serum* from the Friesenhahn Cave, Texas (TMM 933-series).

ANSP 50 is the left upper third premolar, $1P^3$, designated as one of the lectotypes of *M. (S.) mercerii* in the ANSP catalogue and noted without measurements by Cope (1899). Data for *Smilodon* are partly derived from Merriam and Stock (1932), those for "*I.*" *johnstoni* partly from Mawby (1965), and those for *I. crusafonti* and *Ischyrosmilus* sp. from Dr. Björn Kurtén (1982), pers. comm.; other measurements were taken by the author. Measurements are in millimetres; asterisks indicate overlapping ranges of the Port Kennedy specimens with *Smilodon*; "e" indicates an estimation; "w" a worn crown on a tooth; "-" that the dimension is unmeasurable; and "absent" that the character is sometimes not developed.

Elements and Dimensions	*Machaerodus (Smilodon)* specimens *M. (S.) gracilis, M. (S.) mercerii* Port Kennedy Caverns, Pennsylvania ANSP 44 left	ANSP 44 right	ANSP 47 and 50 left	ANSP 47 and 50 right	Size ranges for *Smilodon* derived from Rancho La Brea, California, and Talara, Peru (N) = sample size	*Ischyrosmilus* "*johnstoni*" Cita Canyon, Texas right side	*Ischyrosmilus crusafonti* Broadwater, Nebraska UNSM 25503 left	*Ischyrosmilus* sp. Lisco, Nebraska UNSM 1105 right	Size ranges for *Homotherium* derived from the Friesenhahn Cave, Texas (N) = sample size
						Cast WT 1860			
Length I^1–I^3	21.4e	20.6e			31.8e–23.0 (25)	32.5			42.6–36.2 (6)
Length I^1–P^4	123.4e	129.8e			168.2–134.2 (36)	142.5			155.0–133.0e (2)
Length I^1–M^1	128.8e	-			170.0e–132.5e (20)	-			-

Length of precanine diastema	8.0e	8.0e			17.7–6.9*[1] (50)	10.5			11.6–7.9 (4)
Length C^1–P^4	97.0e	97.9e			131.0–97.0*[2] (34)	114.5			108.4–86.0 (5)
Length of postcanine diastema	12.9e	13.5e			23.6–7.8*[3] (34)	27.7			25.0–8.0 (6)
Length P^3–P^4	49.8	41.5e			65.9–48.8e (32)	-			48.2a–48.0 (2)
I^1 Mesiodistal diameter	5.1	5.2			7.6–5.0*[4] (29)	6.5e			9.9–7.6w (4)
Buccolingual diameter	7.8	7.8			12.7–8.8 (48)	10.7			12.8–9.2 (7)
Crown height	8.9w	8.6w			18.3e–11.6 (35)	-w			17.5w–12.2w (6)
I^2 Mesiodistal diameter	6.4	5.9			9.7–7.3 (30)	9e			12.2–10.0 (9)
Buccolingual diameter	8.8	8.9			14.6–10.1 (54)	12.7			13.2w–10.7 (16)
Crown height	19.9w	-			22.1–16.4 (40)	-w			20.2–16.8 (5)
I^3 Mesiodistal diameter	9.3	9.1			13.2–9.9 (32)	11e			17.5–16.2 (11)
Buccolingual diameter	10.3	10.1			19.0e–13.8 (50)	14.4			12.9–9.8 (19)
Crown height	-	12.0			27.1–18.7 (33)	-w			25.1–17.7 (6)
				ANSP 47					
C^1 Mesiodistal diameter of alveolus	28.0	27.9		27.0	51.0–36.0 (18)	36.5	-	-	35.5–27.7 (3)
Mesiodistal diameter of crown	31.7	-		30.4	44.4e–33.7 (16)	-	29.8	30.3	38.0–30.6 (5)
Buccolingual diameter of crown	13.8	14.2		13.2	24.1–15.3 (14)	16.5	13.5	13.6	14.9–11.6 (5)
Mesial crown height	103.7	-		-	141.4–123.0e (15)				76.7–58.5 (5)
						WT 2429			
Distal crown height	108.8	-		-	151.7–128.3 (14)	93e	-	86	77.5–61.5 (5)
Maximum mesiodistal diameter of root	-	-		28.2	48.9–35.7 (19)	-	-	-	32.8–28.0 (4)
Maximum buccolingual diameter of root	-	-		14.0	22.9–17.3 (18)	-	-	-	15.4–13.5 (4)
			ANSP 50			UCMP 66485			
P^3 Mesiodistal diameter	15.7	15.2	15.8		20.9–12.0*[5] (22)	15.8alv			19.2–9.5alv (3)
Buccolingual diameter	6.8	6.5	7.7		10.6–8.0 (23)	7alv			6.5e–5.8alv (4)
Crown height at protocone	6.8	6.5	8.5		11.6–8.2*[6] (26)	-			9.1–8.2 (2)
			ANSP 47						
P^4 Mesiodistal diameter	30.5e	36.2	-	32.1	46.3–33.4*[7] (26)	40.4			38.6–32.0 (6)
Buccolingual diameter	-	13.2	-	13.7	18.8–11.1 (27)	13.0			12.7–10.0 (8)
Crown height at parastyle	-	7.9w	-	6.1	14.1e–absent*[8] (48)	-			absent
Crown height at paraconule	-	9.8w	-	13.2	24.2e–17.2 (37)	-			13.8–10.0 (4)
Crown height at paracone	-	17.8e	18.2	16.9	27.3–20.6 (30)	-			21.3–17.5w (3)
Crown height at metacone	11.8w	13.3	13.2	13.7	21.6–16.3 (36)	-			17.8–13.7w (4)
Length of metacone blade	13.1	13.2	12.4	12.7	17.6–11.5*[9] (27)	-			15.2–13.1 (4)
M^1 Mesiodistal diameter		-		4.9	7.2–4.7*[10] (8)				6.5alv–5.4alv (2)
Buccolingual diameter	-	-		8.5	15.6–10.3*[11] (9)				5.4alv–3.8alv
Crown height	-	-		3.1	6.0–3.1*[12] (7)				-

Table 4 **Measurements of mandibles and lower permanent dentitions of *Machaerodus (Smilodon) gracilis* and *M. (S.) mercerii* from Port Kennedy Caverns, Pennsylvania, of *Ischyrosmilus ischyrus*, *I. idahoensis*, *I. johnstoni* and *I. crusafonti* from the western States, of *Smilodon gracilis* from Florida and of *Smilodon* from Rancho La Brea, California, and Talara, Peru.**
Measurements were taken by the author except those from Merriam (1918) indicated by "1", Merriam (1905) indicated by "2", from Schultz and Martin (1970) indicated by "3", or by Dr Björn Kurtén (1982, pers. comm.) indicated by "4". Measurements of the teeth of the holotype of *I. idahoensis* are taken from roots and damaged crown. Measurements are in millimetres. "e" indicates an estimation; "w" indicates a worn crown on a tooth; "d" direct measurement across both dentaries; "alv" measurement based on alveolus; "+" indicates a minimal measurement; and "–" that the dimension is not available. Numbered asterisks in right-hand column indicate overlapping size ranges with *Smilodon* from Rancho La Brea and Talara, and are referred to in the text.

Elements and Dimensions	*Machaerodus (Smilodon)* specimens Port Kennedy Caverns, Pennsylvania *M. (S.) gracilis*, ANSP 44 (neotype), 45 and 47 *M. (S.) mercerii*, ANSP 49 and 50 (neotype)					*Ischyrosmilus ischyrus* Merriam, 1905 Holotype UCMP 8140	*Ischyrosmilus idahoensis* Merriam, 1918 Holotype UCMP 22343 Cast AMNH 32797
	ANSP 44 left	ANSP 44 right	ANSP 49 left	ANSP 49 right	ANSP 45, 47, 50		
Length I_1–I_3	15.6e	15.0e	16.1e	16.6e		-	25.5e
Length I_1–C_1	-	22.6e	22.0e	23.9e		-	36.8e
Length I_1–M_1	129.1	112.5e				123.0[1]	(155.0e)
Length I_2–M_1	126.7	112.2e	116.7	110.1		-	152.5e
Length I_2–P_4	-	-	96.1	99.2		-	120.9e
Length C_1–P_4	91.1	-	-	-		-	(107.1e)
Length C_1–M_1	115.9	-	-	-		107.0[1]	(135.2)[1]
Length of postcanine diastema	58.0	-	48.2	48.7		33.5[1], 33.[3]	46.4[1], 46.[3]
Length P_3–M_1	59.9	70.0e	-	-		61.7, 62.4e[3]	71.6, 73.2e[3]
Length of diastema post P_3	8.5e	11.2e	3.6	3.9e		-	4.2
Length P_4–M_1	45.8	48.3e	42.8	42.4		49.8e[3]	57.3e, 58.5[3]
I_1 Mesiodistal diameter	3.9	3.3	-	-		4.0[1]	-
Buccolingual diameter	5.5	5.5	-	-		-	-
Crown height	6.0w	7.8w	-	-		-	-
I_2 Mesiodistal diameter	5.7	5.3	4.9	5.2		6.5[1]	8.5e
Buccolingual diameter	6.9	7.0	5.1	6.7		-	12.7e
Crown height	9.0	8.7w	8.5w	8.2w		-	-
I_3 Mesiodistal diameter	6.5	6.3	6.1	6.2		-	11.5e
Buccolingual diameter	8.9	8.3	8.2	8.2		-	14.0e
Crown height	11.5w	11.9w	11.4w	12.2w		-	-
C_1 Greater crown diameter	10.6	-	11.5	12.5		14.5[1], 15.[3]	19.2[1], 18.[3]
Lesser crown diameter	7.6	-	7.4	8.0		12.5[3]	12.6, 13.5[3]
Buccal crown height	14.8e	-	17.2	16.9		-	-
P_3 Mesiodistal diameter	7.7	-	9.5alv	-		7.0[1], 7.5[3]	10[1], 10.5e[3]
Buccolingual diameter	5.0	-	5.0alv	-		6.5[3]	5.9[1], 6.[3]
Crown height	4.9	-	-	-		-	-
					ANSP 50		
P_4 Mesiodistal diameter	20.7	20.5	20.0	20.0	20.1	20.1[1], 20.5[3]	23.7[1], 24e[3]
Buccolingual diameter	8.7	8.7	8.8	8.9	8.9	12.5[3]	10.4, 10.5[3]
Crown height	13.8	12.8w	13.2	12.8	13.5	-	-

Ischyrosmilus johnstoni Mawby, 1965 Holotype WT 1239 left	right	*Ischyrosmilus crusafonti* Schultz and Martin, 1970 Holotype UNSM 25493	*Smilodon gracilis* Inglis IA, Florida Cast UF 20065	*Smilodon gracilis* Bass Point Waterway, Florida ROM:B numbers	Size ranges for *Smilodon* derived from Rancho La Brea, California, and Talara, Peru (N) = sample size
-	25e				23.5–15.0e*[1] (34)
-	33.5e				35.7–25.0e (34)
-	142e				158.8e–124.6*[2] (26)
-					157.6–123.3e*[3] (33)
-					-
-	112.0		52+		122.8–95.8 (11)
-	128.5		95+		148.7–113.5*[4] (36)
36.5alv	37.0alv	26.9[3]	32.5e		80.2–43.5*[5] (46)
69.8	71.5alv	59.5e[3], 60.0[4]	52e		65.5 (1)
6.4	8.5		3.9		-
48.9	48.5	43.8[3]	38.7		60.9–48.3 (46)
-		5.5e	-		5.6–4.0 (29)
-		6e	-		9.7–7.0 (30)
-		-	-		13.5e–10.5 (29)
				ROM:B 4249	
-		6e	-	6.0	7.8–5.5*[6] (40)
-		8e	-	7.7	10.3–8.3 (40)
-		-	-	9.2	16.8e–10.1 (34)
-		-	-		9.6–7.2 (48)
-		-	-		12.9–10.1 (47)
-		-	-		21.4e–13.5 (45)
				ROM:B 4236	
-	16.5alv	13.7[3], 14.0[4]		11.1	17.6–12.1*[7](19)
-	10e	10.0[3], 11.5[4]	-	7.9	13.8–8.5 (19)
-		-		16.8	24.8–17.9 (15)
13.0	14alv	10[3], 9.5[4]	9alv		10.2–6.5*[8](25)
8.0	6alv	6[3]	6alv		7.1–5.7 (25)
11e	-	-	-		8.3–5.8 (25)
				ROM:B 4229	
22.0	21.8	18.7[3], 19.5[4]	18.6	-	30.9–22.5 (50)
10.3	9.9	9.6[3], 10.0[4]	8.1	8.8	14.6–10.5 (52)
		-	12.6w	-	22.2–16.5 (42)

Table 4 (continued)

Elements and Dimensions	Machaerodus (Smilodon) specimens Port Kennedy Caverns, Pennsylvania M. (S.) gracilis, ANSP 44 (neotype), 45 and 47 M. (S.) mercerii, ANSP 49 and 50 (neotype)					*Ischyrosmilus ischyrus* Merriam, 1905 Holotype UCMP 8140	*Ischyrosmilus idahoensis* Merriam, 1918 Holotype UCMP 22343 Cast AMNH 32797
	ANSP 44 left	ANSP 44 right	ANSP 49 left	ANSP 49 right	ANSP 45, 47, 50		
					ANSP 45		
M_1 Mesiodistal diameter	24.6	24.8	22.8	22.2	25.7	28.5[1], 29.[3]	33.2[1], 33.[3]
Buccolingual diameter	11.4	10.8	10.3	10.5	11.6	15.0?[1], 14.5[2], 16.5[3]	13.5[1], 13.[3]
Crown height paraconid	14.1w	12.7w	12.3w	13.3w	14.6	-	-
Crown height protoconid	13.8w	14.9w	11.8w	12.2w	14.9	-	-
Greater diameter of symphysis	-	-	55.8	50.0		-	70.0
Lesser diameter of symphysis	-	-	15.7	16.5			29.5
					ANSP 45		
Breadth across canine alveoli	-	-	38.2e	36.4e	38.2ed	-	76.2
Breadth across genial flanges	-	-	39.0e	36.7	34.1d	52.0[1]	52.0[1]
Minimum depth in diastema	33.5	34.4	32.3	30.1		-	-
Minimum width in diastema	12.9	9.6	12.5	12.1		-	-
Depth beneath P_3	29.8	33.7	34.0	30.6e		41.4[1]	52.0[1]
Depth mesial to P_4	37.5	32.8e	32.5	32.4		41.2[1], 39.5[3]	49.0[1], 48.[3]
Width mesial to P_4	15.6	12.2e	14.8	14.7		-	22.2[1]
					ANSP 47 left dentary		
Depth at P_4–M_1 contact	32.6	29.3e	32.8	33.2	27.2e	37.5[1], 36.0[2]	-
Width P_4–M_1 contact	16.4	12.7e	15.5	15.8	15.3e	-	21.5
Length from M_1 to coronoid	-	-	-	38.2		-	21.5
Length from I_1 to coronoid	-	-	-	146.4		-	-
Height from coronoid to angle	-	-	-	50.0e		-	-

Ischyrosmilus johnstoni Mawby, 1965 Holotype WT 1239 left	right	*Ischyrosmilus crusafonti* Schultz and Martin, 1970 Holotype UNSM 25493	*Smilodon gracilis* Inglis 1A, Florida Cast UF 20065	*Smilodon gracilis* Bass Point Waterway, Florida ROM:B numbers	Size ranges for *Smilodon* derived from Rancho La Brea, California, and Talara, Peru (N) = sample size
				ROM:B 4260	
28.5w	28.3w	25.8[3], 25.9[4]	20.8	23.0alv	32.1–24.5*[9] (55)
13.8	12.7	12.5[3], 12.4[4]	10.5	10.0alv	17.0–11.8 (57)
-	-	-	14.5w	-	22.2–17.6 (50)
-	-	-	15.0w	-	24.9–16.0 (36)
74e		-	46e	-	78.5–48.7*[10] (48)
19.5		-	14.6	-	36.6–20.9 (50)
64e		-	32e	-	64.6–47.8 (44)
65e		-	44e	-	63.0–40.2 (50)
47.8	46.5	-	28e	-	40.4–27.3*[11] (52)
20.0	18.8	-	11.3	-	21.8–13.8 (52)
42.2	44.5	-	27e	-	41.8–33.3*[12] (26)
43.3	46.5	32.3	25e	-	49.9–32.6*[13] (51)
20.0	20.6	-	13.0	-	25.2–16.5 (51)
44.7	46.0	-	28.7e	-	54.0–33.7 (52)
19.8	20.6	-	14.7	-	25.8–18.8 (52)
-	38.5	-	-	-	-
-	-	-	-	-	209.9–151.0 (30)
83	79.0	-	-	-	77.9–57.1 (42)

Table 5 Measurements of postcranial elements of *Machaerodus (Smilodon) gracilis*, *M. (S.) mercerii*, and *Smilodon*.
Data for *Smilodon* from Rancho La Brea, California, are derived from Merriam and Stock (1932) and from Talara, Peru, from measurements by the author. Measurements are in millimetres; "-" indicates that the dimension is unmeasurable.

Elements and Dimensions	*Machaerodus (S.) gracilis* Port Kennedy Caverns, Pennsylvania ANSP 48		*Machaerodus (S.) mercerii* Port Kennedy Caverns, Pennsylvania ANSP 51				Size ranges for *Smilodon* derived from Rancho La Brea, California, and Talara, Peru (N) = sample size	
Humerus	left		right					
Maximum distal trochlear diameter	67.7		66.0				74.4–54.4e (14)	
Minimum diameter of ulnar articulations	20.9		21.8				36.0–25.2 (25)	
Maximum diameter of shaft over tuber deltoides	31.5		25.0				61.0–38.2 (10)	
Minimum diameter of shaft	24.1		20.7				43.4–30.0 (24)	
Radius	left							
Maximum proximal diameter	34.6						55.5–41.2 (26)	
Minimum proximal diameter	25.3						44.0–31.0 (26)	
Metacarpalia II and III	II right	III right	II left	III left			II	III
Maximum length	-	-	-	77.1			105.0–76.4 (25)	109.6–83.0 (25)
Maximum proximal transverse diameter	17.0	20.8	-	18.4			24.1–18.2 (24)	31.3–24.1 (26)
Maximum proximal dorsoventral diameter	23.0	19.8	-	15.9			34.0–26.4 (24)	29.2–22.8 (24)
Transverse diameter in midshaft	-	-	10.6	11.5			18.8–15.0 (27)	20.0–13.9 (25)
Anteroposterior diameter in midshaft	-	-	9.5	10.9			17.8–13.9 (27)	16.7–12.3 (25)
Transverse diameter of distal end	-	-	-	18.4			23.1–13.9 (27)	24.5–20.2 (20)
Metacarpalia IV and V			IV left	IV right	V left	V right	IV	V
Maximum length			-	-	60.1	-	107.4–79.4 (17)	86.6–61.6 (21)
Maximum proximal transverse diameter			16.8	13.0	15.5	15.5	26.6–18.9 (19)	28.8–20.1 (21)
Maximum proximal dorsoventral diameter			-	15.9	17.3	16.5	28.7–20.6 (19)	32.2–23.3 (21)
Transverse diameter in midshaft			10.4	-	9.5	-	16.3–12.3 (19)	17.9–12.9 (21)
Anteroposterior diameter in midshaft			10.1	-	10.6	-	16.6–12.2 (20)	16.1–10.8 (21)
Transverse diameter of distal end			-	-	15.4	-	22.9–19.5 (11)	21.9–19.1 (15)
Calcaneum	right	right						
Maximum length	83.2	-					106.8–79.4 (20)	
Maximum width across astragalar facet	31.6	30.7					44.2–32.7 (22)	
Maximum width across cuboid facet	23.9	24.8					44.2–32.5 (21)	
Maximum width over sustentaculum	34.2	34.8					54.4–40.4 (23)	

Astragalus	right		
Maximum width	48.0		61.2–46.0 (31)
Maximum length	48.2		61.2–45.8 (33)
Minimum diameter of neck	21.0		29.5–21.0 (31)
Maximum diameter of head	25.1		38.0–26.7 (30)

Metatarsalia II, III, and V	II	II	III	V	V	II	V
	left	right	right	left	right		
Maximum length	72.6	-	-	-	-	96.5–73.7 (27)	94.8–70.8 (32)
Maximum proximal transverse diameter	13.7	14.3	-	16.5	15.4	19.0–13.5 (28)	27.0–18.8 (26)
Maximum proximal dorsoventral diameter	20.9	23.5	-	12.8	12.9	32.4–25.2 (27)	28.6–17.2 (33)
Transverse diameter in midshaft	10.9	-	11.5	-	9.9	16.0–11.5 (31)	14.3–10.1 (31)
Dorsoventral diameter in midshaft	10.0	-	11.9	-	8.4	15.8–12.3 (30)	16.9–10.6 (32)
Transverse diameter of distal end	16.8	-	16.8	-	-	20.8–16.8 (22)	20.5–15.3 (26)

Table 6

Parts A and B Measurements of recently recovered materials of *Ischyrosmilus gracilis* from Bass Point Waterway I, Sarasota County, and El Jobean Pit, Charlotte County, Florida; and of the astragali from Port Kennedy, Pennsylvania, and from Haile Locality XVA, Alachua County, Florida, from Robertson (1976).

Measurements in parentheses for ANSP 48 are from Cope (1899). Measurements are in millimetres; "e" indicates an estimated measurement; "alv" indicates measurement of alveolus; "w" a worn crown on a tooth; and "-" that the measurement is unavailable.

Part A, Dental Materials	*Ischyrosmilus gracilis* ROM:B numbers Bass Point Waterway I			*Ischyrosmilus gracilis* ROM:B 8400, left maxilla El Jobean Pit
Upper Dentition	ROM:B 4235	ROM:B 4237		
I^3	right	left		
Mesiodistal diameter	9.1	8.5		
Buccolingual diameter	10.2	10.1		
Crown height	15.7	13.8		
Crown-root length	39.9	-		
	ROM:B 4228			
C^1	right			
Mesiodistal diameter	23.0			28.0alv
Buccolingual diameter	11.1			14.0alv
	ROM:B 4235		ROM:B 4253	
Length of postcanine diastema	10.6	9.7	9.5	8.0

Table 6 (continued)

Part A. Dental Materials	*Ischyrosmilus gracilis* ROM:B numbers Bass Point Waterway I		*Ischyrosmilus gracilis* ROM:B 8400, left maxilla El Jobean Pit
Upper Dentition (continued)			
	ROM:B 4225	ROM:B 4234a	
P^3	left	right	
Mesiodistal diameter	17.0	16.2	17.3
Buccolingual diameter	7.0	7.4	7.1
Crown height	10.0	9.1	6.5w
	ROM:B 4230		
P^4	right		
Mesiodistal diameter	34.2		30.5
Buccolingual diameter	11.9+		12.7
Crown height of parastyle	absent		5.7w
Crown height of paraconule	13.8		9.5w
Crown height of paracone	19.1		11.6w
Crown height of metacone	14.2		8.7w
Length of metacone blade	14.0		12.1
Lower Dentition	ROM:B 4249		
I_2	left		
Mesiodistal diameter	6.0		
Buccolingual diameter	7.9		
Crown height	9.8		
Crown-root length	30.6		
	ROM:B 4236	ROM:B 4250	
C_1	left	left	
Greater (?mesiodistal) crown diameter	11.1	11.1	
Lesser (?buccolingual) crown diameter	7.9	8.5	
Crown height on buccal surface	16.8	-	
Crown-root length	48.4	48e	
	ROM:B 4229		
P_4	right		
Mesiodistal diameter	-		
Buccolingual diameter	8.8		
Crown height	-		
	ROM:B 4229		
M_1	right		
Mesiodistal diameter	23.0alv		

Buccolingual diameter	10.0alv
Crown height of paraconid	-
Crown height of protoconid	-

Part B. Postcranial Elements	*Smilodon gracilis* UF 17496, right astragalus Haile XVA	*Ischyrosmilus gracilis* ROM:B numbers Bass Point Waterway I			*Machaerodus (S.) gracilis*, ANSP 48, right astragalus Port Kennedy Caverns, Pennsylvania
Astragalus			ROM:B 4238 left		
Maximum length	41.6		42.4		48.2 (48)
Maximum transverse diameter	45.2		44.4		48.0 (38)
Transverse diameter of trochlear	28.7		26.3		(27)
Maximum diameter of neck	-		19.4		21.0 (17)
Maximum diameter of head	26.6		26.5		25.1 (25)
Minimum diameter of head	18.7		21.2		
External elevation of trochlear	21.1		26.0		(22)
Metatarsalia III and IV		ROM:B 4233 III left	ROM:B 6574 III right	ROM:B 4232 IV left	
Length		-	-	94.9	
Transverse diameter of proximal end		20.8	22.2	17.3	
Dorsoventral diameter of proximal end		25.4	29.3	22.2	
Transverse diameter in midshaft		12.4	12.8	10.5	
Dorsoventral diameter in midshaft		12.7	12.0	12.8	
Transverse diameter of distal end		18.3	18.6	15.9	
Dorsoventral diameter of distal end		-	-	14.8	
Transverse diameter of phalangeal articulation		-	-	13.8	
Proximal Phalanx			ROM:B 4100 ?right		
Length			37.1		
Transverse diameter of proximal end			15.1		
Dorsaoventral diameter of proximal end			13.2		
Transverse diameter of shaft			11.4		
Dorsoventral diameter in midshaft			8.0		
Transverse diameter of distal end			12.4		
Dorsoventral diameter of distal end			9.0		
Transverse diameter of distal articulation			10.7		

Table 7 Measurements of postcranial elements assigned to *Ischyrosmilus johnstoni* by Mawby (1965) and size ranges of *Homotherium serum* (Meade, 1961) from Friesenhahn Cave, Texas, Rancho La Brea, California, and Talara, Peru.

Measurements were derived from Merriam and Stock (1932) and from measurements taken by the author. "e" indicates an approximate measurement.

Elements and Dimensions	*Ischyrosmilus johnstoni* Cita Canyon, Texas			Size ranges for *Homotherium serum* Friesenhahn Cave, Texas (N) = sample size	Size ranges for *Smilodon* derived from Rancho La Brea, California, and Talara, Peru (N) = sample size
Humerus	WT 625	UCMP 66487	WT 1691		
Length from caput to medial condyle	319.0			358.0–340.0 (3)	385.0–309.0 (15)
Transverse diameter at midshaft	23.3			33.0–28.5 (4)	43.4–30.0 (24)
Anteroposterior diameter at midshaft	35.9			49.0–39.4 (4)	61.0–38.2 (24)
Transverse diameter of distal epiphysis	70.4	71.7		84.4–82.5 (3)	128.3–93.7 (22)
Minimum anteroposterior diameter of trochlear	27.0	25.0	27.3	30.7–29.5 (3)	36.0–25.3 (25)
Ulna	WT 628				
Maximum transverse diameter of olecranon	30.3				48.0–33.6 (17)
Anteroposterior diameter in middle of semilunar notch	31.7			45.2,45.0 (2)	
Anteroposterior diameter over coronoid process	58.4				78.8–57.3 (22)
Length of semilunar notch	33.8				
Length of radial notch	32.0				
Femur	WT 1066	UCMP 66488			
Length over greater trochanter to distal condyles				353.0–338.0 (5)	408.0–317.0 (17)
Length from caput femoris to medial condyle	405e				
Maximum proximal diameter over caput and greater trochanter	95e			95.7–89.1 (5)	108.8–79.5 (18)
Anteroposterior diameter of caput femoris	42.9	43.2		42.8–41.0 (5)	50.7–39.1 (20)
Transverse diameter at midshaft	37.7	36.1e		31.7–30.0 (5)	40.4–29.6 (20)
Anteroposterior diameter at midshaft	29.4	29.4		28.8–27.2 (5)	35.4–26.8 (20)
Transverse diameter of distal epiphysis	73.9			73.5–67.4 (5)	90.2–65.2 (19)
Anteroposterior diameter of distal epiphysis	75.2			71.0–67.0 (5)	80.3–63.9 (29)
Transverse diameter of patellar (rotular) surface	34.4				60.0–41.9 (18)
Transverse diameter of lateral condyle	22.8				
Transverse diameter of medial condyle	28.9			32.5–21.0 (5)	36.0–24.9 (18)
Maximum transverse diameter of intercondylar notch	15.0			15.5–13.0 (5)	23.3–14.5 (19)
Minimum transverse diameter of intercondylar notch	10.0				
Tibia		UCMP 66489			
Maximum length		345.0		297.0–265.0 (3)	305.0–239.0 (14)
Transverse proximal diameter		78.7		76.0e,71.6 (2)	90.4–75.2 (14)
Transverse diameter at midshaft		30.5		28.0–26.2 (3)	33.0–25.1 (16)
Transverse diameter of distal epiphysis		52.0		55.6–50.1 (3)	63.3–45.0 (14)
Anteroposterior diameter of distal epiphysis		36.0		38.0–30.0 (3)	41.5–33.3 (20)

Literature Cited

ADAMS, G. I.
1896 The extinct Felidae of North America. American Journal of Science, Ser. 4, 1:419–444.

BARBOUR, E. H. and H. J. COOK
1915 A new saber-toothed cat from Nebraska. Nebraska Geological Survey 4:235–239.

BERTA, A. and H. GALIANO
1983 *Megantereon hesperus* from the Late Hemphillian of Florida with remarks on the phylogenetic relationships of machairodonts (Mammalia, Felidae, Machairodontinae). Journal of Paleontology 57:892–899.

BIELAWSKI, J. B.
1905 Gisement et faune de Rocca Negra à Perrier. Revue d'Auvergne 1905:297–304.

BOVARD, J. F.
1907 Notes on Quaternary Felidae from California. University of California Publications, Bulletin of the Department of Geology 5:155–170.

BROWN, B.
1908 The Conard Fissure, a Pleistocene bone deposit in northern Arkansas: with descriptions of two new genera and twenty new species of mammals. Memoirs of the American Museum of Natural History 9:158–208.

CHURCHER, C. S.
1966 The affinities of *Dinobastis serus* Cope 1893. Quaternaria 8:263–275.

COPE, E. D.
1880 On the extinct cats of North America. American Naturalist 14:833–858.
1893 A new Pleistocene saber-tooth. American Naturalist 27:876–879.
1895 The Fossil vertebrata from the fissure at Port Kennedy, Pa. Proceedings of the Academy of Natural Sciences of Philadelphia for 1895:446–451.
1899 Vertebrate remains from Port Kennedy bone deposit. Journal of the Academy of Natural Sciences of Philadelphia, Ser. 2, 11:193–267.

CROIZET, J.-B. and A.-C.-G. JOBERT
1828 Recherches sur les ossements fossiles du département du Puy-de-Dôme. Paris, (n.p.). 224 pp.

DE BONIS, L.
1976 Un félidé à longues canines de la colline de Perrier (Puy-de-Dôme): ses rapports avec les félines machairodontes. Annales de Paléontologie, Vertébrés 62:159–198.

EVERNDEN, J. F., D. E. SAVAGE, G. H. CURTIS, and G. T. JANE
1964 Potassium-argon dates and the Cenozoic mammalian chronology of North America. American Journal of Science 262:145–198.

FABRINI, E.
1890 I *Machairodus (Meganthereon)* del Valdarno superiore. Bollettina Comitato Geologico d'Italia 21:121–144, 161–177.

GERVAIS, P.
1878 Sur la dentition des smilodons. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences de Paris 87:582–583.

GILL, T.
1872 Arrangement of the families of mammals and synoptical tables of characters of the subdivisions of mammals. Smithsonian Miscellaneous Collections 11:1–98.

GRAY, J. E.
1821 On the natural arrangement of vertebrose animals. London Medical Repository 15:296–310.

GREGORY, J. T.
1942 Pliocene vertebrates from Big Spring Canyon, South Dakota. University of California Publications, Bulletin of the Department of Geological Sciences 26:307–446.

HARRISON, J. A.
1983 The Carnivora of the Edson Local Fauna (Late Hemphillian), Kansas. Smithsonian Contributions to Paleobiology, No. 54:1–42.

HAY, O. P.
1920 Description of Pleistocene vertebrates found in the United States. Proceedings of the United States National Museum 58:83–146.
1927 The Pleistocene of the Western Region of North America and its vertebrated animals. Carnegie Institution of Washington, Publication 322:1–346.

HIBBARD, C. W.
1952 Vertebrate fossils from late Cenozoic deposits of central Kansas. University of Kansas Paleontological Contributions, Vertebrata, Article 2:1–14.
1955 Notes on the microtine rodents from the Port Kennedy cave deposit. Proceedings of the Academy of Natural Sciences of Philadelphia 107:87–97.

JOHNSTON, C. S. and D. E. SAVAGE
1955 A survey of various late Cenozoic vertebrate faunas from the Panhandle of Texas. Part 1, Introduction, description of localities, preliminary faunal lists. University of California Publications in Geological Sciences 31:27–49.

KAUP, J. J.
1833 Description d'ossements fossiles de mammifères inconnus jusqu'à présent qui se trouvent au Muséum grand-ducal de Darmstadt. Second cahier: carnassiers fossiles. Darmstadt, Heyer. 31 pp.

KLEIN, J.
1971 The ferungulates of the Inglis Ia local fauna, early Pleistocene of Florida. M.Sc. Thesis, University of Florida. 115 pp.

KITTS, D. B.
1957 A Pliocene vertebrate fauna from Ellis County, Oklahoma. Oklahoma Geological Survey, Circular 45:1–27.

KURTÉN, B.
1962 The sabre-toothed cat *Megantereon* from the Pleistocene of Java. Zoologische Medelingen 38:101–104.

1963 Notes on some Pleistocene mammal migrations from the Palaearctic to the Nearctic. Eiszeitlater und Gegenwart 14:96–103.

1965 The Pleistocene Felidae of Florida. Bulletin of the Florida State Museum, Biological Sciences 9:215–273.

KURTÉN, B. and E. ANDERSON

1980 Pleistocene mammals of North America. New York, Columbia University Press. 442 pp.

KURTÉN, B. and M. CRUSAFONT PAIRÓ

1977 Villafranchian Carnivores (Mammalia) from La Puebla de Valverde (Teruel, Spain). Commentationes Biologicae 85:1–39.

LEIDY, J.

1868 Notice of some vertebrate remains from Hardin County, Texas. Proceedings of the Academy of Natural Sciences of Philadelphia for 1868:174–176.

1889 The sabre-tooth tiger of Florida. Proceedings of the Academy of Natural Sciences of Philadelphia for 1889:29–31.

LUND, P. W.

1842 Blik paa Brasiliens Dyreverden för sidste Jordomvaeltning. Danske Videnskabernes Selskabs Skrifter, Naturvidenskabelig og Mathematisk Afhandling 9:137–208.

LUNDELIUS, E. L., JR., C. S. CHURCHER, T. DOWNS, C. R. HARINGTON, E. LINDSAY, G. SCHULTZ, H. A. SEMKEN, S. D. WEBB and R. J. ZAKRZEWSKI

In press The North American Plio-Pleistocene sequence. Berkeley, University of California Press.

LYDEKKER, R.

1884 Indian Tertiary and Post-Tertiary Vertebrata. Siwalik and Narbada Carnivora. Palaeontologia Indica, Ser. 10, 2:178–355.

MARTIN, L. D.

1980 Functional morphology and the evolution of cats. Transactions of the Nebraska Academy of Sciences 7:141–154.

MARTIN, L. D. and C. B. SCHULTZ

1975 Cenozoic mammals from the Central Great Plains. Part 5, Scimitar-toothed cats, *Machairodus* and *Nimravides*, from the Pliocene of Kansas and Nebraska. Bulletin of the University of Nebraska State Museum 10:55–63.

MATTHEW, W. D.

1918 Contributions to the Snake Creek fauna; with notes upon the Pleistocene of Western Nebraska; American Museum Expedition of 1916. Bulletin of the American Museum of Natural History 38:183–229.

MAWBY, J. E.

1965 Machairodonts from the late Cenozoic of the Panhandle of Texas. Journal of Mammalogy 46:573–587.

MEADE, G. E.

1961 The saber-toothed cat, *Dinobastis serus*. Bulletin of the Texas Memorial Museum 2:23–60.

MERRIAM, J. C.

1905 A new sabre-tooth from California. University of California Publications, Bulletin of the Department of Geology 4:171–175.

1915 Extinct faunas of the Mohave Desert, their significance in the study of the origin and evolution of life in America. Popular Science Monthly 86:245–264.

1917 Relationships of Pliocene mammalian faunas from the Pacific Coast and Great Basin provinces of North America. University of California Publications, Bulletin of the Department of Geology 10:421–443.

1918 New mammals from the Idaho Formation. University of California Publications, Bulletin of the Department of Geology 10:523–530.

1919 Tertiary mammalian faunas of the Mohave Desert. University of California Publications, Bulletin of the Department of Geology 11:437a–437e, 438–585.

MERRIAM, J. C. and C. STOCK

1932 The Felidae of Rancho La Brea. Carnegie Institution of Washington, Publication 422:1–231.

OSBORN, J. F.

1918 Equidae of the Oligocene, Miocene and Pliocene of North America, iconographic type revision. Memoirs of the American Museum of Natural History, n.s. 2:1–330.

PILGRIM, G. E.

1931 Catalogue of the Pontian Carnivora of Europe in the Department of Geology. London, British Museum of Natural History. 174 pp.

PIVETEAU, J.

1961 Carnivora. *In* Piveteau, J., ed., Traité de paléontologie. Paris, Masson, t.6, vol. 1, pp. 641–820.

RAWN-SCHATZINGER, V. M. and R. O. COLLINS

1981 Scimitar cats, *Homotherium serum* Cope from Gassaway Fissure, Annon County, Tennessee, and the North American distribution of *Homotherium*. Journal of the Tennessee Academy of Science 56:15–19.

ROBERTSON, J. S.

1976 Latest Pliocene mammals from Haile XVA, Alachua County, Florida. Bulletin of the Florida State Museum, Biological Sciences 20:1–18.

SCHAUB, S.

1925 Ueber die Osteologie van *Machaerodus cultridens* Cuvier. Eclogae Geologicae Helvetiae 19:225–266.

1934 Observations critiques sur quelques Machairodontides. Eclogae Geologicae Helvetiae 27:99–406.

SCHULTZ, C. B. and L. D. MARTIN

1970 Machairodont cats from the early Pleistocene Broadwater and Lisco local faunas. Bulletin of the University of Nebraska State Museum 9(2):1–56.

SCHULTZ, C. B., M. R. SCHULTZ, and L. D. MARTIN

1970 A new tribe of saber-toothed cats (Barbourofelini) from the Pliocene of North America. Bulletin of the University of Nebraska State Museum 9(1):1–31.

SIMPSON, G. G.

1941 The function of saber-like canines in carnivorous mammals. American Museum Novitates 1130:1–12.

1945 The principles of classification and a classification of mammals. Bulletin of the American Museum of Natural History 85:1–350.

SLAUGHTER, B. H.

1960 A new species of *Smilodon* from a late Pleistocene alluvial terrace deposit of the Trinity River. Journal of Paleontology 34:486–492.

1963 Some observations concerning the genus *Smilodon* with special reference to *Smilodon fatalis*. Texas Journal of Science 15:68–81.

STOLL, N. R., R. Ph. DOLLFUS, J. FOREST, N. D. RILEY, C. W. SABROSKY, C. W. WRIGHT, and R. V. MELVILLE, eds.

1961 International code of zoological nomenclature adopted by the 15th International Congress of Zoology. London, Published for the International Commission on Zoological Nomenclature by the International Trust for Zoological Nomenclature. 176 pp.

TEILHARD DE CHARDIN, P.

1939 On two skulls of *Machairodus* from the Lower Pleistocene beds of Choukoutien. Part 1, The *Machairodus* of Locality 13. Bulletin of the Geological Society of China 19:235–256.

TEILHARD DE CHARDIN, P. and P. LEROY

1945 Les félidés de Chine. Publications de l'Institut de Géobiologie 11:1–58.

TEILHARD DE CHARDIN, P. and J. PIVETEAU

1930 Les mammifères fossiles de Nihowan. Annales de Paléontologie 19:1–134.

WEBB, S. D.

1974 The status of *Smilodon* in Florida. *In* Webb, S. D., ed., Pleistocene mammals of Florida. Gainesville, University Presses of Florida, pp. 149–153.

WOODWARD, A. S.

1898 Outlines of vertebrate palaeontology for students of zoology. Cambridge, Cambridge University Press. 470 pp.

ZDANSKY, O.

1924 Jungtertiäre Carnivoren Chinas. Palaeontologia Sinica, Ser. C, 2:1–153.

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